도시계획학 박사학위논문

Network Analyses of Habitat Connectivity for Biodiversity of Urban Forest Birds, Forest Mammals, and a Threatened Tree Species

생물다양성 보전을 위한 서식지 연결성의 네트워크 분석:
도시 산림성 조류와 산림성 포유류, 음나무를 대상으로

2013년 8월

서울대학교 환경대학원
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강완모의 박사학위논문을 인준함
2013년 7월

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Abstract

Network Analyses of Habitat Connectivity for Biodiversity of Urban Forest Birds, Forest Mammals, and a Threatened Tree Species

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Assessing and maintaining connectivity among habitats are key components of conserving species in fragmented landscapes. However, little work has examined how and to which degree the connectivity of habitats support abundant and diverse wildlife communities, or whether connectivity of habitat networks can maintain broad-scale ecological processes, such as dispersal and gene flow, in South Korea. In this regard, the effects that habitat connectivity has on distribution patterns of species diversity, wildlife movement, and gene flow in heterogeneous landscapes were investigated in this dissertation.

In the dissertation, I have primarily focused on three main taxa with different movement abilities: urban forest birds, forest mammals, and populations of a tree species (*Kalopanax septemlobus*). Forest birds and mammals are more mobile than plants, but pollen and seeds may be unexpectedly dispersed long distances by wind or animals. In addition, forest mammals are generally less mobile than forest birds. These organisms are key representatives of biodiversity in terrestrial ecosystems; they play an important role in ecosystem functions because

they provide valuable and vital ecosystem services. However, the organisms and their habitats are constantly threatened by human activities and urbanization.

Because habitat requirements and movement abilities are species-specific, the responses of various species to landscape and environmental changes are diverse and complex. Thus, multivariate statistical techniques combined with graph based approaches were employed to examine multi-scale species–habitat relationships, focusing on the links between habitat connectivity and species diversity.

First, I assessed the effects of habitat, landscape factors, and human disturbance on the diversity of urban forest bird communities. Second, I investigated the influence of connectivity of protected forest area networks, road characteristics, and topographic and landscape features on three different groups of road-killed forest mammals, including small, intermediate, and large ones. I also examined the potential barrier effects of roads and rivers on protected area networks of each mammal group. Finally, I analyzed climate and topographic factors associated with *K. septemlobus* distribution and predicted gene flow and genetic diversity in populations of *K. septemlobus* using connectivity models.

Patch size exerted a positive influence on the diversity of most bird functional groups, and it had the greatest effects on both total abundance and species richness of birds. Vegetation complexity had positive effects on the total species richness and abundances of migrant and ground-nesting birds. Remnant patches with lower levels of human disturbance had higher bird species diversity than newly established patches where intense human activities occurred more frequently. In addition, habitat connectivity was a critical factor that influenced the total abundance of all species and the diversity of functional groups, including

resident, bush-nesting, insectivore, and edge species. Management strategies for the conservation of urban forest birds, therefore, should consider not only local improvements in habitat structure – through increased patch size, reduced human disturbance, and increased vegetation complexity – but also the maintenance of habitat connectivity.

In all three mammal groups, the number of roadkill was higher when inter-patch connections were intersected by roads, indicating that roadkills occur mainly on roads that pass through dispersal or movement routes with high connectivity. Without considering the barrier effects of roads and rivers, the protected area network was well-connected for large mammals, whereas the network seemed to be less connected and consisted of many isolated areas for intermediate and small mammals. However, examination of barrier effects revealed that the network connectivity for large mammals was greatly decreased by the potential barriers. These results suggest the importance of securing movement paths and corridors that cross barriers such as roads and rivers in order to conserve large mammals. Small mammal would benefit from the creation of new habitats that connect existing protected areas.

Annual mean temperature was the most important factor in determining the distribution of *K. septemlobus*, indicating that the species is vulnerable to thermal stress. The spatial genetic structure of *K. septemlobus* populations was best explained by a patch-based representation of a habitat network. The trees' genetic structure and diversity were highly correlated with habitat connectivity at scales of a few kilometers, revealing that spatial habitat configuration at the landscape scale is important in structuring populations. The current habitat network seemed to be well connected to maintain landscape-scale gene flow, but climate change is

expected to reduce the levels of habitat connectivity. Therefore, it is needed to consider improving and maintaining habitat connectivity in order to sustain *K. septemlobus* metapopulations, as well as to regulate the over-exploitation of species.

This dissertation presents three landscape ecological network analyses that provide significant insights for biodiversity conservation and management. I argue here that connectivity of habitat networks for forest birds, mammals, and a tree species is a key factor affecting patterns of species distribution, migration, and population structure, in spite of the fact that these species groups have different habitat selection and movement characteristics. Hence, quantifying the degree to which a landscape facilitates or impedes ecological processes among habitat patches for a given species or species group is essential to inform conservation and management decisions. In addition, these analyses have shown that graph based multi-scale network models can be effectively applied to predict and explain ecological processes related to habitat connectivity. Overall, this dissertation suggests that landscape management strategies require restoring and maintaining habitat connectivity across a variety of scales. Habitat connectivity enables natal dispersal, recolonization of unoccupied habitats, and metapopulation persistence in the short to medium term, while it conserves genetic diversity for adaptive evolution in the long term.

Keywords: Gene flow, Graph theory, Habitat fragmentation, Landscape connectivity, Roadkill

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CHAPTER 1: Background and objectives

1.1 Background and scope of the research

1.1.1 Biodiversity: Importance and threats

Biological diversity (i.e., Biodiversity) refers to the full range of variety and variability of plants, animals, and micro-organisms at the genetic and species levels as well as various types of ecosystems in which they occur (UNCED 1992; Koski et al. 1997). Biodiversity is generally influenced by climate, resource availability, and disturbance regimes, and the changes in biodiversity may affect not only species traits but also the structures and functioning of an ecosystem such as ecosystem productivity, decomposition and nutrient cycling, and intra– and inter–specific competition, coupled with cascading effects on food web (Hector et al. 1999; Schläpfer and Schmid 1999; Chapin et al. 2000; Cardinale et al. 2006). Such interactive process between biodiversity and ecosystem processes provides ecosystem services that make vital contributions to human well-being (Millenium Ecosystem Assessment 2005). As the magnitude and stability of ecosystem services are strongly related with changes in biodiversity, it is important to note that biodiversity (i.e., the functional traits, richness, abundance, and distribution ranges of species) is influenced by different environmental conditions (Chapin et al. 2000). In this regard, a number of governmental agencies, organizations, and even citizens around the globe, all of whom are interested in conserving biodiversity, are deeply concerned about environmental degradation which affects the stability and sustainability of ecosystem services (Groom et al. 2006; Van Dyke 2008).

Since the 1992 United Nations Convention on Biological Diversity (UNCBD), long–term persistence of biodiversity has been a main goal of most

environmental management and conservation plans by local and national governments, particularly as a key concept for maintaining ecosystem services (UNCED 1992; Gaston et al. 2002; Wiersma and Nudds 2006). For example, ecologists and conservation planners now focus on both maximizing the number of species and monitoring umbrella species in protected areas (Lawler et al. 2003). In particular, protected areas such as nature reserves and national parks have high diversity of both habitats and species, and may serve as a source habitat (Naughton-Treves et al. 2005). On the other hand, urban as well as agricultural landscapes comprise semi–natural habitats in the form of remnant woodlands and groves, hedgerows, windbreak forests, and field margins. These semi-natural habitats provide habitat areas at a local scale that may be considered the elements of corridors or stepping stones at a regional scale (Tscharntke et al. 2005; Colding et al. 2006). Because various semi–natural habitats can also increase vertical habitat complexity that contributes to habitat diversity (Marshall and Moonen 2002), the semi–natural habitats are valuable for conserving biodiversity. In a broader perspective, parks and reserves linked by semi-natural habitats could form a valuable network at which many organisms can coexist as metapopulations (Hanski 1998; Naughton-Treves et al. 2005).

However, protected areas have been isolated from semi-natural habitats over the last decades due to rapid urbanization (Hansen et al. 2005; Hilty et al. 2006). Urbanization, defined as the outward expansion of built–up area, is now considered one of the biggest threats to biodiversity (Wilcove et al. 1998). In particular, roads crossing landscapes in urban areas cause both habitat destruction and fragmentation (Forman and Alexander 1998). In other words, the road–crossing landscapes in expanded cities have resulted in habitat loss and homogenized vegetation structure within-patch level, with increased habitat isolation within-landscape level, as the spatial and functional connectivity between

natural and semi-natural habitats decreases (Hilty et al. 2006). Such threats may be intensified by the combined effects of habitat fragmentation and climate change (Opdam and Wascher 2004).

The forest area in South Korea was reported at 63,688 km^2 in 2010 (Korea Forest Service 2012). Forest area was decreased by about 53 km^2 per year from 2000 to 2010. Although natural disaster, particularly forest fire, may also cause forest loss, the major driver of forest loss is mainly considered the indiscriminate change in land use and urbanization (DeFries et al. 2010; Kang et al. 2012a). While it is challenging to achieve large–scale afforestation in South Korea, it is essential and feasible to identify sites for habitat creation and to restore and maintain habitat networks by considering the spatial configuration of protected areas and semi–natural habitats (Bengtsson et al. 2003; Lee and Thompson 2005). Furthermore, for long–term biodiversity conservation, ecologists and conservation planners need to know how species respond to environmental changes accelerated by rapid urbanization at various spatial and temporal scales. In doing so, research on ecological and evolutionary processes such as dispersal, gene flow, and traits of species related to range shift will play an important role in guiding conservation efforts (West et al. 2009).

1.1.2 Landscape connectivity

Understanding how species are spatially and genetically distributed within a network of fragmented habitat patches is crucial for biodiversity conservation. Species responses to landscape and environmental changes are diverse and complex, owing to species–specific habitat–use and habitat requirements (Clergeau et al. 2006; McKinney 2006). Species persistence in fragmented landscapes, however, is commonly dependent on landscape connectivity (Soulé 1986; Donnelly

and Marzluff 2006). Landscapes with high connectivity offer habitats for various wildlife species and allow long–term species persistence, through gene flow in animal and plant populations as well as the rescue effect (Soulé 1986; Hanski 1994; Tischendorf and Fahrig 2000; Brooks 2003; Verbeylen et al. 2003).

Landscape connectivity can be defined as the degree to which the spatial arrangement of the landscape facilitates or impedes movement, dispersal, and gene flow among habitat patches (Taylor et al. 1993). Landscape connectivity may be approached in two different ways (Calabrese and Fagan 2004; Baguette and Van Dyck 2007): functional connectivity, which refers to the degree of interaction among patches based on actual movement of organisms (Fagan and Calabrese 2006); and structural connectivity, which describes the physical relations between landscape patches in terms of their spatial configuration (Keitt et al. 1997).

Functionally well-connected metapopulations are expected to be resilient to stochastic demographic processes (Opdam et al. 2006). Thus, when evaluating species persistence, it is necessary to measure the level of functional connectivity by analyzing species' movement responses to landscape spatial structure (Urban and Keitt 2001). However, it is challenging to obtain sufficient data on the related themes across large heterogeneous landscapes (Rudnick et al. 2012). On the other hand, structural connectivity can be used to infer the potential for dispersal (Bodin and Norberg 2007). Therefore, integrating the data on movement and gene flow gained from field experiments into modeling and measurements of landscape structure (i.e., structural connectivity) is an effective approach when assessing functional connectivity (Fall et al. 2007; Rudnick et al. 2012).

1.1.3 Multi-scale concept and graph-based network analysis

At a micro–evolutionary time scale, the persistence of species requires the

ability to escape and disperse from long–term changes in environmental conditions (e.g., climate change) (Holt 1990). The movement capacity of organisms is generally an important determinant of ecological phenomena on an ecological timescale of one generation (Wiens et al. 1993). This emphasizes that species movement patterns may suggest crucial, ecological and evolutionary implications for the persistence of biodiversity. Hence, the understanding of the relationships among movement patterns of organisms, habitat fragmentation, and landscape structure will help to predict species extinction risks owing to urbanization and climate change.

Species require different needs for the amount of habitats in the landscape (Hansson and Angelstam 1991). In addition, because species possess different movement behaviors and gap–crossing abilities, i.e., dispersal abilities, they demand different spatial configurations of habitats within the landscape. For this reason, protected area networks may be perceived as well–connected by a certain species or a group of species, but may not be suitable for the other species or group. In this regard, designing protected–area networks based on a single umbrella species (typically far-ranging large mammals) may not be sufficient to ensure long-term persistence of biodiversity. Therefore, conservation planning must be simultaneously established at multiple spatial scales in order to achieve multi–species conservation (Minor and Lookingbill 2010).

Multi–scale connectivity is typically analyzed with methods in graph theory, a branch of discrete mathematics dealing with networks (Urban et al. 2009; Minor and Lookingbill 2010). A landscape network or graph is a set of nodes with edges between them, where nodes are the landscape elements, and the edges, i.e., where inter-node links, represent paths or connectivity (Minor and Urban 2007). A graph-based network analysis is an efficient tool for not only assessing the physical relationships among habitat patches (i.e., structural connectivity) but also

examining how the movement of organisms is affected by these relationships within a landscape (i.e., functional connectivity), with modest data requirements (Calabrese and Fagan 2004; Urban et al. 2009).

Networks can be defined at different levels of spatial scale. Thus, it can be used to determine whether habitat networks allow for dispersal and gene flow both theoretically and empirically; and at which spatial scale connectivity is correlated with species diversity. In landscape ecology, many researchers have recently developed various graph-based metrics and models to measure habitat connectivity (Laita et al. 2011). In addition, ecologists can develop and employ more sophisticated graph-based network analysis, when graph–based landscape metrics are combined with the methods developed in other advanced network-oriented studies such as social network studies (e.g., Bodin and Norberg 2007; Estrada and Bodin 2008; Bodin and Saura 2010; Kang et al. 2012b).

1.2 Research objectives and questions

Habitat network with a high level of connectivity allows dispersal and recolonization of patches that are necessary for long-term species persistence (Hanski 1994). Thus, the understanding of how a species, populations, or communities respond to landscape structure at varying scales and of whether their habitat networks are resilient to forest fragmentation and climate change are crucial in order to implement effective biodiversity conservation and management plans (Taylor et al. 1993). However, little attention has been given to examine the contributing factors to connectivity in South Korea such as the definite range of spatial scales that are important in determining spatial patterns of species distribution and the role of biosphere reserves and semi-natural forests in enhancing biodiversity and species persistence.

The main objective of this dissertation, therefore, was to investigate relationships between spatial patterns of species distributions, habitat connectivity, and ecological processes in heterogeneous landscapes. I have primarily focused on three main taxa with different movement (or dispersal) abilities: urban forest birds, forest mammals, and populations of a tree species (*Kalopanax septemlobus*). When it comes to movement abilities, animals, especially forest birds and mammals, are generally more mobile than plants, even though pollen and seeds may be dispersed unexpectedly great distances by animals or wind. In terms of movement abilities of animals, forest birds are likely to be more mobile than forest mammals. On the whole, these three organisms, namely forest birds, mammals, and plants, all play an important role as key biodiversity surrogates in terrestrial ecosystems in securing and enhancing the capacity of natural processes, i.e., ecosystem functions, which ultimately provide valuable ecosystem services. However, human activities and urbanization have continuously threatened the organisms and their habitats, and it is therefore critical to investigate such anthropogenic impacts on the organisms and ecosystems in urban areas.

In the present study, multivariate statistical techniques combined with graph based multi-scale approaches were used to study the effects of habitat and landscape factors on the diversity of bird communities, the roadkill distribution of forest mammals, and finally the gene flow of plant populations. Integrated insights for biodiversity conservation at the genetic and species levels can be derived from three network analyses, which allow the investigation of the relationships between habitat connectivity and ecological processes of forest birds, mammals, and a tree species with very different movement characteristics. The findings of this study may offer some insights into management implications so as to contribute to the diversity and persistence of species. The six main questions with regard to three main research sections in the presented work are:

○ **Forest bird assemblages in an urban environment (Chapter 2)**

– How do local habitat characteristics and human disturbances interplay with landscape connectivity to influence diversity of forest bird communities in an urban environment?

– What is the relative importance of habitat characteristics, human disturbance, and landscape connectivity in predicting species richness and abundance of forest birds in an urban area?

○ **Effects of connectivity of protected area networks and roads on forest mammals (Chapter 3)**

– Are protected area networks correlated with the roadkills of forest mammals in South Korea?

– What is the potential impact of barriers, such as highways and rivers, on landscape connectivity for forest mammals?

○ **Habitat connectivity and gene flow of *K. septemlobus* (Chapter 4)**

– Which kind of connectivity metrics is correlated with gene flow in populations of *K. septemlobus*?

– Which scale level of connectivity is most associated with the population genetic structure of *K. septemlobus*?

1.3 Dissertation outline

The primary objective of this dissertation was to improve our understanding of the function of ecological processes in determining spatial patterns of species, in order to ensure long-term conservation of species. This chapter (Chapter 1) formulates the general scope of the dissertation and research questions.

Chapter 2, 3, and 4 focus on the research questions of connectivity conservation and habitat restoration interests. Chapter 2 examines the effects of habitat, landscape variables, and human disturbance on urban forest bird communities. In Chapter 3 roadkill distribution of forest mammals is estimated by measuring connectivity among protected areas. Chapter 4 investigates the relationships between habitat connectivity and gene flow for a sparsely-distributed tree, *Kalopanax septemlobus* (Araliaceae). Finally, the general summary and conclusions of this dissertation are presented in the conclusion section. A summary of the work, i.e., the abstract of the dissertation, is given in both English and Korean (Abstract and 국문초록).

CHAPTER 2: Effects of habitat structure, human disturbance, and landscape connectivity on urban forest bird communities

2.1 Introduction

Rapid urbanization has become an important area of concern in biodiversity conservation, as urban development and human disturbance accelerate habitat destruction and species extinction (Shochat et al. 2006). As a result of increased population combined with the movement of people from rural to urban areas, more than half of the world's population lives in towns and cities (UN 2012). Consequently, the ecological footprint of urban areas has almost reached the ecosystem's carrying capacity, while many cities are still in the process of developing action plans to reduce their ecological footprint (Wu 2010). However, in a landscape with a slightly less extreme level of urbanization, green space components (e.g., remnant forests, parks, and gardens) can still harbor diverse wildlife species (Goddard et al. 2010). In addition, these components and species living in the green spaces of urban areas can provide urban dwellers with a wide range of socio-economic benefits (Colding et al. 2006; Sadler et al. 2010). Thus, to achieve the sustainability of urban ecosystem services, the integrated understanding of the knowledge with regard to urban biodiversity and the current management practices of urban green spaces has become very important.

The understanding of how urban nature and biodiversity respond to human-caused landscape changes is crucial for enhancing their ecological performances. It is well known that the structure, composition, and spatial configuration of urban green spaces influence biodiversity, its ecological functions, and, hence, ecosystem services that the biodiversity provides (Sadler et al. 2010).

However, most urban planning efforts and ecological research to conserve urban biodiversity have mainly concentrated on protected natural areas or large green patches, despite the fact that most green spaces in cities are often small, scattered, and fragmented (Matteson and Langellotto 2010). Indeed, it is reported that small urban green space's ecosystem functions, especially biodiversity value, are not adequately explored (e.g., Shwartz et al. 2013).

Although small green spaces may not provide abundant resources and refuges for various wildlife species as larger patches, they can form a well–connected network that increases the urban biodiversity (Shanahan et al. 2011). In addition, the environment of biodiversity friendly green space may enable urban people to enjoy amenity services, such as aesthetic enjoyment and recreation (Kong et al. 2007). Thus, in the context of spatial configuration of urban landscape, understanding how to plan and manage small green spaces to maintain, or even increase, biodiversity can be of great value for urban residents, as well as urban planners and policy-makers.

This study investigates how local habitat structures and human disturbance interplay with landscape connectivity to influence urban bird diversity. This research focused on forest bird assemblages in small patches (<20 ha) as they are known as ecological indicators of habitat structure and human disturbance (O'Connell et al. 2000). Compared to other vertebrates, birds are easy to monitor and provide a mechanism to examine urban effects varied across a gradient of urban development (Koskimies 1989; Minor and Urban 2010). The objectives of this study were to examine how local habitat characteristics, human disturbance, and landscape configuration influence the diversity of bird guilds of small forest patches embedded in an urban landscape; and to assess the relative importance of these variables for species diversity. These questions and findings may invite ecologists and urban planners to develop more thoughtful guidelines on how to

design and manage a more sustainable urban ecosystem.

2.2 Materials and methods

2.2.1 Study area and bird surveys

The study was conducted in Seoul and surrounding cities in Gyeonggi Province, most densely populated places in the world with a population of over ten million people (Statistics Korea 2012). About 30% of the study area is covered by forests (Korea Forest Service 2012), and urban remnant forest patches are under pressure of rapid changes in land use (Kim 2003). Small forest patches (n=44) between 0.5 and 20.0 ha in size were identified to be embedded in the urban and suburban areas (Fig. 2-1). In order to avoid spatial autocorrelation biases, the patches were separated by a minimum distance of 1 km (Legendre et al. 2002).

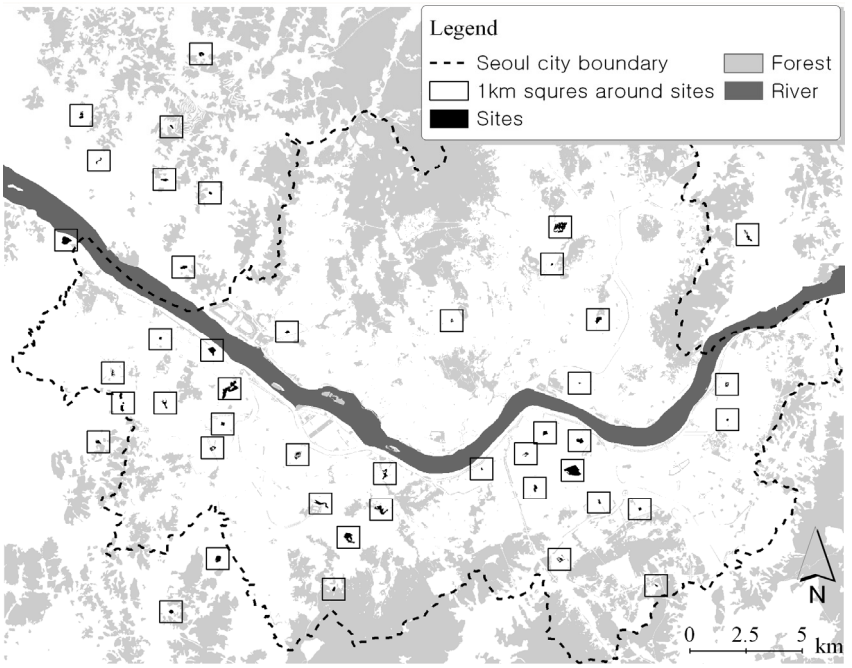

Fig. 2-1. Map of Seoul and surrounding area with the study sites. Forest patches are shaded.

In 2012, four repeat bird surveys at each patch were conducted using a line transect method (Bibby et al. 2000), three times during the breeding season (April-July) and once during the non-breeding season (September-October), between 30 min before sunrise and 4 h after (a total of 176 surveys). All birds heard or seen within the patch areas were recorded. Double-counting of mobile birds was considered a minor issue, since the observer was continually on the move. When birds were observed, the species type and the number of individuals were recorded. Birds just flying over the site were not included in the count. Urban exploiters (such as House Sparrow *Passer domesticus*, Common Pigeon *Columba livia*, and Magpie *Pica pica*) were also excluded because they are usually associated with human-created environments (de Toledo et al. 2012). For the

purpose of analysis, estimates of species diversity were derived for each patch: species richness (total number of recorded bird species within each survey patch) and species abundance (average number of individuals counted across all surveys at a patch). To investigate the effects of habitat characteristics, landscape variables, and human disturbance on the bird assemblage, each observed species, according to Lee and Park (1995); field observation; and expert opinion, was assigned to various functional groups based on migratory, nesting and foraging strategy, diet, and habitat use, as well as species rarity (Table 2-1). Diet guild was assigned based on the main foods eaten in the breeding season.

Table 2-1. Bird species included in this study and their functional guilds.

Common name	Species name	# of obs.	Species rarity	Migratory status	Nesting guild	Foraging guild	Diet	Habitat use
Asian Brown Flycatcher	*Muscicapa dauurica*	2	Com	Migrant	Canopy	Canopy	Ins	*
Asian Stubtail	*Urosphena squameiceps*	1	Com	Migrant	Ground	Bush	Ins	Interior
Barn Swallow	*Hirundo rustica*	7	Com	Migrant	House	Aerial	Ins	*
Black-naped Oriole	*Oriolus chinensis*	34	Com	Migrant	Canopy	Canopy	Ins	Edge
Blue-and-white Flycatcher	*Cyanoptila cyanomelana*	6	Com	Migrant	Ground	Canopy	Ins	Interior
Brown-eared Bulbul	*Hypsipetes amaurotis*	343	Com	Resident	Canopy	Canopy	Omn	Generalist
Bull-headed Shrike	*Lanius bucephalus*	1	Com	Resident	Canopy	Canopy	Ins	Edge
Chinese Nuthatch	*Sitta villosa*	2	Rare	Migrant	Hole	Canopy	Ins	Interior
Chinese Sparrowhawk	*Accipiter soloensis*	1	Com	Migrant	Canopy	*	Car	Edge
Coal Tit	*Parus ater*	11	Com	Resident	Hole	Canopy	Ins	Interior
Common Cuckoo	*Cuculus canorus*	11	Com	Migrant	*	*	Ins	Generalist
Common Kestrel	*Falco tinnunculus*	9	Com	Resident	House	*	Car	*
Daurian Redstart	*Phoenicurus auroreus*	23	Com	Resident	House	Canopy	Ins	Edge
Dollarbird	*Eurystomus orientalis*	6	Rare	Migrant	Canopy	Canopy	Ins	Edge
Eastern Crowned Willow Warbler	*Phylloscopus coronatus*	33	Com	Migrant	Ground	Canopy	Ins	Interior
Eurasian Hobby	*Falco subbuteo*	1	Rare	Migrant	Canopy	*	Car	Edge
Eurasian Jay	*Garrulus glandarius*	41	Com	Resident	Canopy	Canopy	Omn	Generalist
Eurasian Nuthatch	*Sitta europaea*	9	Com	Resident	Hole	Canopy	Ins	Interior
Goldcrest	*Regulus regulus*	10	Com	Migrant	Canopy	Canopy	Ins	Interior
Great Spotted Woodpecker	*Dendrocopos major*	57	Com	Resident	Hole	Canopy	Ins	Interior

Common name	Species name	# of obs.	Species rarity	Migratory status	Nesting guild	Foraging guild	Diet	Habitat use
Great Tit	*Parus major*	289	Com	Resident	Hole	Canopy	Ins	Edge
Grey-backed Thrush	*Turdus hortulorum*	3	Com	Migrant	Canopy	Ground	Ins	Interior
Grey-headed Woodpecker	*Picus canus*	20	Com	Resident	Hole	Canopy	Ins	Edge
Grey-streaked Flycatcher	*Muscicapa griseisticta*	5	Com	Migrant	*	*	Ins	*
Japanese Pygmy Woodpecker	*Dendrocopos kizuki*	52	Com	Resident	Hole	Canopy	Ins	Interior
Jungle Crow	*Corvus macrorhynchos*	17	Com	Resident	Canopy	Canopy	Omn	Generalist
Long-tailed Tit	*Aegithalos caudatus*	69	Com	Resident	Canopy	Canopy	Ins	Interior
Marsh Tit	*Parus palustris*	249	Com	Resident	Hole	Canopy	Ins	Interior
Mugimaki Flycatcher	*Ficedula mugimaki*	8	Com	Migrant	*	Canopy	Ins	*
Orange-flanked Bush Robin	*Tarsiger cyanurus*	8	Com	Migrant	*	*	Ins	Interior
Oriental Cuckoo	*Cuculus saturatus*	1	Com	Migrant	*	*	Ins	Generalist
Oriental Turtle Dove	*Streptopelia orientalis*	144	Com	Resident	Canopy	Ground	Gra	Edge
Pale Thrush	*Turdus pallidus*	4	Com	Migrant	Canopy	Ground	Ins	Interior
Ring-necked Pheasant	*Phasianus colchicus*	25	Com	Resident	Ground	Ground	Gra	Interior
Rufous-tailed Robin	*Luscinia sibilans*	21	Com	Migrant	*	*	Ins	*
Rustic Bunting	*Emberiza rustica*	1	Com	Migrant	Ground	Bush	Ins	Edge
Siberian Blue Robin	*Luscinia cyane*	3	Com	Migrant	Ground	Bush	Ins	Interior
Tristram's Bunting	*Emberiza tristrami*	4	Com	Migrant	Ground	Bush	Ins	Interior
Varied Tit	*Parus varius*	53	Com	Resident	Hole	Canopy	Ins	Interior
Vinous-throated Parrotbill	*Paradoxornis webbianus*	282	Com	Resident	Bush	Bush	Ins	Edge
White-backed Woodpecker	*Dendrocopos leucotos*	1	Com	Resident	Hole	Canopy	Ins	Interior
White's Thrush	*Turdus dauma aureus*	9	Com	Migrant	Canopy	Ground	Ins	Interior
Winter Wren	*Troglodytes troglodytes*	2	Com	Resident	Ground	Ground	Ins	Interior
Yellow-browed Warbler	*Phylloscopus inornatus*	39	Com	Migrant	*	Canopy	Ins	Interior
Yellow-rumped Flycatcher	*Ficedula zanthopygia*	2	Rare	Migrant	Hole	Canopy	Ins	Interior
Yellow-throated Bunting	*Emberiza elegans*	6	Com	Resident	Ground	Ground	Ins	Interior

Species rarity *Com* common, *Rare* rare species

Diet *Car* carnivore, *Gra* granivore, *Ins* insectivore, *Omn* omnivore

*Species were omitted for guild characterization due to the peculiarity of breeding habit or non-breeders

2.2.2 Variables measured

Local-scale habitat characteristics

Local habitat attributes, including patch area, vegetation complexity, and presence of feral cats, were measured. A forest-cover map for the study area was derived from a biotope map (Seoul Metropolitan Government 2010). The biotope map was originally created by Seoul metropolitan government using aerial photograph and satellite imagery interpretation, and was later classified according to ground-truthed data. In order to accurately estimate patch area, the edges of the patch were digitized using the combination of a forest map and aerial photograph (dated from May 2011) of 0.5 m resolution provided by Daum Communications Corp.

Complexity in vegetation structure and composition, which supports more habitat diversity, are important predictors of bird diversity (Joshi et al. 2012). Hence, the vegetation characteristics of patch sites were surveyed from September to October 2012. A 100 m transect was placed within each site, and the survey was conducted to 2 m both sides of this line, giving a total survey area of 400 m^2. The number of transects per patch was based on patch area: 1 transect for <10 ha patches and 3 transects for 10-20 ha patches (Miller and Cale 2000). Transect measurements of each >10 ha patch were averaged to obtain an overall estimate. The documented records include species identity and stem diameter for all woody plant species greater than 5 cm diameter at breast height (DBH) within the transect. Percent cover of vegetation, leaf-litter, and woody debris were estimated at 2-m intervals along the transect. Canopy cover was estimated using a densitometer. Presence/absence of shrub, grass, litter layer, and coarse and fine woody debris were also recorded. The resulting vegetation variables were:

(i) Tree (>5 m height), shrub (1-5 m height), and total woody species richness per 400 m^2;
(ii) Woody stem density per 400 m^2;
(iii) Total basal area and basal area of hardwood, conifer, and shrub per 400 m^2;
(iv) Mean of individual woody species basal areas per 400 m^2;
(v) Estimates of percent cover of vegetation, leaf-litter, and woody debris (canopy, >5 m height; shrub, 1-5 m height; grass, 0-1 m height; leaf-litter; fine woody debris, 1-10 cm diameter; coarse woody debris, >10 cm diameter)

Principal coordinate analysis (PCoA) (Legendre and Legendre 1998) based on a Bray–Curtis similarity distance was performed to combine these multiple vegetation characteristics into fewer explanatory variables. The PCoA is an ordination technique, which has an advantage over principal component analysis (PCA). For instance, in PCoA, any ecological distance can be applied, while it is only allowed to use Euclidean distance as a similarity measure in PCA. In the study, two-dimensional PCoA was implemented by the package labdsv in R (Roberts 2010). The first and second PCoA axes explained 67.9% of the total variance in vegetation characteristics. The resulting first and second scores of the ordination were referred as 'Vege complexity 1' and 'Vege complexity 2' (Shanahan et al. 2011). The total basal area and basal area of hardwood and shrub; percent cover of shrub, leaf-litter, and fine and coarse woody debris; total woody and shrub plant richness; and woody stem density showed a positive correlation with Vege complexity 1, while the mean of individual woody species basal areas was negatively correlated with Vege complexity 1 (Pearson's r) ($p < 0.05$). Vege complexity 2 showed positive correlations with percent cover of shrub, of leaf-litter, and of fine and coarse woody debris; total woody, tree, and shrub species richness; and mean of individual woody species basal areas (Pearson's r) ($p < 0.05$). Thus, two vegetation complexity measures indicated a gradient of vegetation diversity

and basal area heterogeneity.

Very little work has focused on the effects of non-vegetation components, such as cats, on forest bird assemblages in urban areas. Nevertheless, feral cats are known as predators for birds (Rodríguez-Estrella et al. 1991), so the presence/absence of feral cats at each site was also documented during the bird surveys.

Human disturbance

Patch type and human population density were included as human disturbance factors influencing bird species richness and abundance. In terms of patch type, two main types of patch are considered: newly established and remnant native forest patches. The remnant patches in urban areas are sites that have never been cleared for urban development with less human visits. On the contrary, newly established forest patches are vegetation-covered sites that have been created and planted with trees, which are mainly urban parks in the study area. Newly established and remnant patches differed in the severity of human disturbance, as the number of visitors is the major driver that could disturb bird species (Fernández-Juricic and Tellería 2000). For example, newly established sites have more than 500 visitors per day, while there were relatively a few visitors (i.e., less than 50 people per day) to remnant patches (W. Kang, *personal observation*). In the study, a remnant patch was coded as 0 and a newly established patch as 1. Population density was also calculated by summing the number of residents within a 1km buffer around the edges of each patch using the BIZ-GIS database (http://www.biz-gis.com/GISDB), based on the 2005 population and housing census in South Korea (KSIS 2005).

Landscape variables

Normalized difference vegetation index (NDVI) was chosen as this approach is strongly related to the amount of vegetation cover (Purevdorj et al. 1998), estimated from 15-m ASTER imagery from May 9, 2012. NDVI values were classified in thirteen classes ranging from zero (concrete structures) to twelve (high-density vegetation) (Shwartz et al. 2013). The average green proportion for five buffer zones (100–500 m) around a patch was then calculated.

Patch connectivity at a landscape level was also measured, using a graph-theoretical approach. The connectivity measure was based on the probability of connectivity (PC; see a more detailed description in Saura and Pascual-Hortal (2007)). PC is defined as the probability that two points (organisms) placed randomly in a landscape fall into habitat areas that are reachable from each other (interconnected), given a set of habitat patches and links among them (Saura and Pascual-Hortal 2007). In order to compute PC and its fractions, the links between every two patches i and j first need to be characterized by the probability of dispersal (p_{ij}), here obtained as a negative exponential function of the Euclidean distance between patches (Bunn et al. 2000; Urban and Keitt 2001). A dispersal probability of 0.05 was defined to correspond to the threshold dispersal distance (i.e., the cut-off distance, if exceeded a patch pair have no link). The path with the maximum product probability (p_{ij}^{*}) is considered the best possible one to conduct the dispersal movement of individuals from patch i to j through the network of patches (see Saura and Rubio (2010) for further details). The importance of patch as a stepping stone between other patches is estimated through the *dPCconnector* fraction derived from the PC metric (Saura and Rubio 2010). A certain patch will have a *dPCconnector* value that is greater than zero only when, first, it is part of the best (i.e., maximum product probability) path used for dispersal movements between other patches in a landscape; and, second, when, after losing that patch,

the alternative paths between the remnant patches that are available cannot compensate for the connecting role played by that patch in an intact landscape (Bodin and Saura 2010). The *dPCconnector* was calculated at the distance thresholds of 0.5 km, 1 km, 1.5 km, 2 km, 3 km, and 5 km for every patch of the study area. Since these mean NDVI and *dPCconnector* values were highly correlated, hierarchical partitioning (Mac Nally 2002) was performed to select the variables that had the greatest independent influence on bird species richness and abundance, i.e., the mean NDVI in a 100 m buffer zone around a patch and *dPCconnector* at the distance threshold of 500 m.

South and north sides of the study area are separated by the Han River with a width of approximately 1km (Fig. 2-1). Thus, a dummy-coded dispersal barrier variable was also included. South side was coded as 1 and north side as 0. In addition, *dPCconnector* scores were graphically presented to compare connectivity of the south side to that of north side.

2.2.3 Data analyses

First, a Mantel test (Mantel 1967) with the package vegan in R (Oksanen et al. 2008) was used so as to examine spatial autocorrelation in overall bird species richness and abundance at the patch sites. The Mantel test is a method to assess the correlation between two distance matrices. For the present research one matrix was the geographic distance between pairs of patch sites, and the other was the Bray–Curtis dissimilarity index between site pairs, which was calculated for both species richness and mean abundance.

Seventeen separate generalized linear models (GLMs) were performed, using a log link function assuming a Poisson distribution, to explore the relative influence of local and landscape level variables, and human disturbance on bird

diversity. For the abundances of long distance migrant, bush nester, and bush foraging guild, it was assumed that a negative binomial distribution and a logarithmic link function was used in order to explain over-dispersion in the observed data. The Poisson and negative binomial models were implemented using the package stats (Chambers and Hastie 1992) and MASS (Venables and Ripley 2002), respectively, in R (R Core Team 2013). No analysis was conducted for species richness in each guild and abundance of house nesters, which nest on man-made structures such as gutters and eaves, aerial foragers, and carnivores, as there was an insufficient number of species or individuals (i.e., almost no individuals of those guilds were recorded in majority of study sites) (Table 2-1).

A model-averaging approach was adopted based on information criteria for model selection (Burnham and Anderson 2002). First, all models were ranked according to the AICc (corrected Akaike Information Criterion) using the MuMIn package in R (Barton 2011). Variables included in the most parsimonious models with △AICc values below 4 were identified by averaging their estimated coefficients and associated standard errors weighted by each model's AICc (Burnham and Anderson 2002). Finally, coefficients and standard errors for the variables that had p-values <0.05 were presented. Except vegetation complexity measures and dummy variables all measurements were log-transformed (log[x + 1]) to improve normality. Before executing multivariate regressions, multicollinearity among independent variables was tested by performing Pearson's correlations, and it was found that no variables were strongly correlated (i.e., $|r| < 0.6$).

Alongside a model-averaging procedure, this study used a hierarchical partitioning approach in which all possible variable combinations are assessed to quantify the independent contribution of each explanatory variable, so as to explain variation in each of the response variables total species richness and bird abundance (Chevan and Sutherland 1991). Also, R-squared (r^2) was used as a

goodness-of-fit measure. A randomization procedure was performed with 1,000 iterations to determine the statistical significance of independent effects (Mac Nally 2002). The package hier.part in R was used in the analysis (Walsh and Mac Nally 2008).

2.3 Results

During the field research, 46 bird species and 1,925 individuals were observed (Table 2-1). Although the majority of the birds sampled were common species, four rare migrant species with 11 individuals were also observed. The observed species were almost evenly divided between migrants and residents. Also, fifteen species were canopy nesters, 11 were hole nesters, one was a bush nester, and nine were ground nesters. Twenty-five species were canopy foragers, five were bush foragers, and seven were ground foragers. The majority of the species were classified as insectivores, while two species were granivores and three were omnivores. More species preferred interior habitat or were forest edge specialists than were habitat generalists.

From the mantel test results, it is indicated the study sites could be considered statistically independent. For both total species richness and bird abundance data, spatial autocorrelation across the sites was very weak or non-existent, with a non-significant correlation coefficient ($p > 0.05$) between the geographic distance and the species richness and bird abundance difference matrices ($r = 0.009$; $r = -0.012$, respectively).

Local habitat, landscape variables, and human disturbance explained the variance of the total species richness, bird abundance, and abundances of different guilds. Among the local habitat characteristics, patch area was positively correlated to the diversity of bird guilds, except for the migrant, ground-foraging, and

granivore bird guilds (Table 2-2). Vege complexity 2 showed positive effects on the total species richness and abundances of migrant and ground-nesting birds (Table 2-2). The presence of feral cats in urban forest fragments was positively correlated with the total abundance of birds and the insectivore bird abundance (Table 2-2). Two landscape variables exerted strong influences on the attributes of urban forest bird communities. *dPCconnector* measured at a distance threshold of 500 m had positive effects on the total bird abundance and abundances of resident, bush-nesting, insectivore, and edge species (Table 2-2). Dispersal barrier factor influenced only the edge species abundance. Forest edge species were statistically more commonly found in the north side of the study area than in the south side (Table 2-2).

Patch type, which is classified according to the presence or levels of human disturbance, was also found to be important in explaining the variance of both richness and abundance of birds. For example, the total species richness and abundance were significantly higher in the remnant patches than in the newly established forest patches (Table 2-2). Furthermore, resident, canopy-, hole-, and bush-nesting, bush- and ground-foraging, insectivore and granivore, and edge species were more common in the remnant patches. Another notable finding was that the north side of the study area had more well-connected urban fragments and more conservation-priority areas as key connectors than those in the south side (Fig. 2-2). On the contrary, Vege complexity 1, mean NDVI 100 m, and human population density showed no significant influence on bird species diversity (Table 2-2).

Patch area was the most important variable that could predict the total species richness, followed by patch type and Vege complexity 2 (Fig. 2-3a). It also showed the greatest effect on the total bird abundance, followed by patch type, *dPCconnector* 500 m, and the presence of feral cats (Fig. 2-3b).

Table 2-2. Estimated average coefficients±SE for local structural, landscape variables, and human disturbance (i.e., *p*-values <0.05) for the most parsimonious (△AICc <4) generalized linear models with Poisson or negative binomial error.

Variable type	Total richness	Total abundance	Migratory status		Nesting guild			
			Migrant	Resident	Canopy	Hole	Bush	Ground
Distribution error	Poisson	Poisson	Negative binomial	Poisson	Poisson	Poisson	Negative binomial	Poisson
Adjusted R^2	0.86	0.98	0.21	0.98	0.66	0.79	0.51	0.31
Intercept	-0.38±0.52	-1.42±0.47	-1.66±1.82	-1.62±0.51	-2.56±0.78	-2.55±0.76	-5.14±2.35	-5.07±2.61
Local structural								
Area	0.55±0.12	0.80±0.11	–	0.82±0.12	0.84±0.19	0.86±0.18	0.96±0.44	1.12±0.52
Vege complexity 1	–	–	–	–	–	–	–	–
Vege complexity 2	2.47±1.16	–	6.91±3.19	–	–	–	–	10.47±4.77
Cat presence	–	0.19±0.09	–	–	–	–	–	–
Landscape								
Mean NDVI 100 m	–	–	–	–	–	–	–	–
dPCconnector 500 m	–	366.06±141.28	–	462.41±145.48	–	–	1159.75±547.18	–
Dispersal barrier	–	–	–	–	–	–	–	–
Human disturbance								
Patch type	-0.49±0.17	-0.56±0.13	–	-0.58±0.15	-0.43±0.21	-0.52±0.21	-2.43±0.82	–
Population density	–	–	–	–	–	–	–	–

Table 2-2. (continued).

Variable type	Foraging height guild			Feeding guild			Habitat use		
	Canopy	Bush	Ground	Insectivore	Granivore	Omnivore	Interior	Edge	Generalist
Distribution error	Poisson	Negative binomial	Poisson	Poisson	Poisson	Poisson	Poisson	Poisson	Poisson
Adjusted R^2	0.90	0.51	0.40	0.97	0.32	0.51	0.78	0.92	0.50
Intercept	-1.90±0.56	-5.99±2.23	-1.69±1.39	-1.94±0.59	-0.80±0.81	-4.01±1.05	-3.61±0.83	-1.60±0.77	-3.80±1.02
Local structural									
Area	0.90±0.13	1.06±0.44	–	0.85±0.14	–	1.04±0.22	1.13±0.18	0.63±0.18	1.02±0.22
Vege complexity 1	–	–	–	–	–	–	–	–	–
Vege complexity 2	–	–	–	–	–	–	–	–	–
Cat presence	–	–	–	0.27±0.11		–	–	–	–
Landscape									
Mean NDVI 100 m	–	–	–	–	–	–	–	–	–
dPCconnector 500 m	–	–	–	466.69±159.54		–	–	762.07±196.71	–
Dispersal barrier	–	–	–	–	–	–	–	-0.36±0.13	–
Human disturbance									
Patch type		-2.43±0.82	-1.53±0.56	-0.57±0.17	-1.45±0.53	–	–	-1.04±0.25	–
Population density	–	–	–	–	–	–	–	–	–

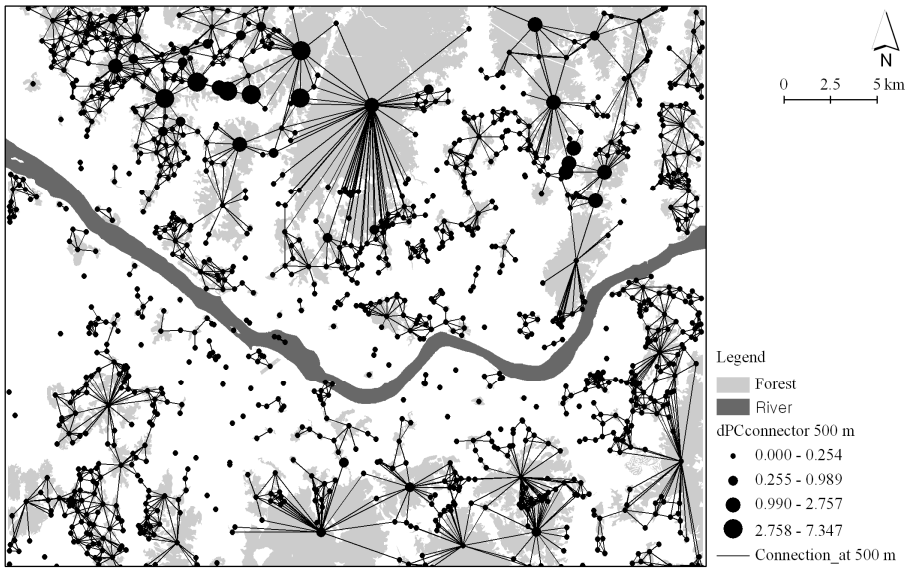

Fig. 2-2. Forest map and network representation of the study area. Forest patches connected by black lines are assumed to be connected via species movement based on a 500-m maximum dispersal distance (Circles that represent patches are scaled by their *dPCconnector* scores measured at the distance threshold of 500 m).

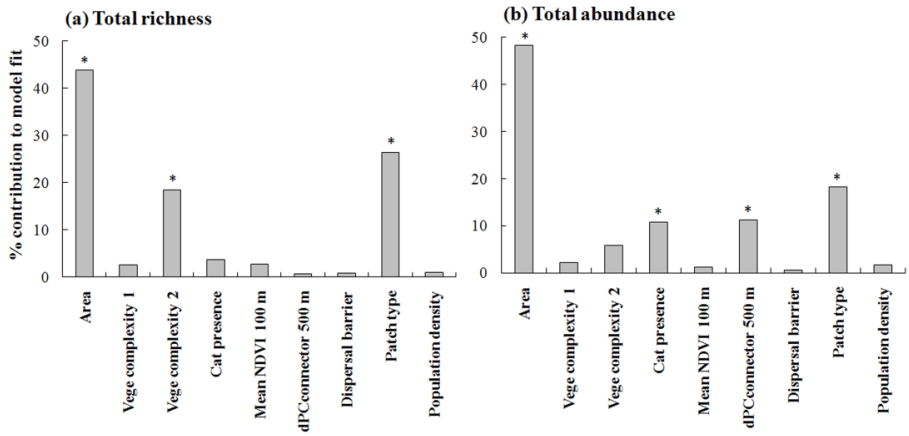

Fig. 2-3. The independent contribution of each variable to model fit for (a) the total bird species richness and (b) abundance data, as determined by hierarchical partitioning. The model includes all nine independent variables indicated in the figure. An asterisk (*) indicates the variables for which its independent percentage contribution to overall model fit was significant at $p < 0.05$.

2.4 Discussion and conclusions

Conserving biodiversity in urban areas has become a high priority for conservation action (Alvey 2006). The results showed that even small (<20 ha) forest patches in a highly urbanized and densely populated region can support a significant functional diversity of bird communities. The birds recorded in this study corresponded to nearly 70% of the forest birds sampled in 10 urban forests of which size is over 100 ha each, in the Seoul region (Park and Lee 2000). In addition, the birds sampled accounted for 60% of the total forest bird species observed in the continuous non-disturbed deciduous forest (ca. 2,240 ha) in central Korea (Choi et al. 2006a). More importantly, rare migrant species were also detected in the small urban forest fragments, even though the majority of forest birds sampled were common species. Both rare and common species are essential

for biodiversity conservation, since they all contribute to ecosystem functioning that is strongly connected to the urban ecosystem health (Lyons et al. 2005; Gaston 2010). The co-occurrence of rare and common species represents that small forest patches not only shelter groups of common species but also act as stepping stones that facilitate the movement of rare migrant species within the urban landscape. This implication raises management issues for the small forest patches within urban environments where both rare and common species inhabit.

The positive influence of patch area on the diversity of most functional groups of bird species (Table 2-2) is notable, as it had the greatest effects on both overall species richness and abundance (Fig. 2-3). In fact, some studies have already suggested that patch area is the best predictor of bird species richness and diversity in vegetation fragments (e.g., Drinnan 2005). This strong relationship between patch area and bird community diversity is related to a size threshold of 20-30 ha, the point at which species richness and abundance rapidly decline (MacDonald and Kirkpatrick 2003). In this regard, only a small range of patch sizes (0.5–20 ha) was considered in the study area, and the patch area indeed appeared to have the greatest effect on both the total species richness and abundance (Fig. 2-3). Again, it is, therefore, feasible to conclude that small changes in the areas of urban forest remnants may increase the species richness and functional diversity of birds.

However, forest habitats in urban areas, especially small patches, generally experience a higher degree of human use compared to rural forests. Such use leads to direct disturbance, through activities such as walking either on or off trails, which can be detrimental to forest bird species (Fernández-Juricic 2004). The patch type related to human disturbance in the study also showed negative effects on the diversity and abundance of birds (Table 2-2). Patch type was the second most influential factor for both the overall species richness and abundance (Fig. 2-

2). Remnant patches with a low level of human disturbance had higher species diversity than newly established patches where more human activities occurred. In particular, the abundances of bush–nesting and bush– and ground–feeding species, which are expected to be most heavily affected by human disturbance, were negatively correlated to patch type. This can be well explained by the relationship between the frequency of human visitation and the frequency of resource use by forest birds, such as foraging, breeding, and roosting. In other words, high levels of human visitation to urban forest fragments may decrease their temporal and spatial resource availability particularly throughout the breeding seasons (Fernández-Juricic 2000b). As human intrusion into habitats increases, the chances of colonization would decrease, which may lead an increase in the probabilities of functional homogenization of bird communities characterized by a higher proportion of exotic or disturbance–tolerant species (Devictor et al. 2007).

Furthermore, vegetation complexity can increase forest bird species richness (Husté et al. 2006; Evans et al. 2009). In general, mature trees and high complexity of vegetation cover provide more diverse habitats (Karr and Roth 1971). Especially in urban habitats, the presence of a shrub layer has been shown to be particularly important to bird species diversity, especially low-nesting species (Burr and Jones 1968; Tilghman 1987). In the study, a positive effect of the vegetation complexity variable was found, which was positively correlated with the percent cover of shrub and the mean of basal area of trees, on the total species richness and the abundances of migrant and ground-nesting birds (Table 2-2). The vegetation complexity would increase the probabilities of the occupation of ground/tree-hole and ground/tree species, presumably because of a higher degree of the availability of diverse feeding and nesting resources (Fernández-Juricic 2000a). Thus, it is recommended to increase the vegetation complexity of urban forest fragments when aiming at improving local bird diversity.

Spatial arrangement of habitat fragments is another crucial point to consider for the movement and dispersal of species in landscapes where a habitat comprises less than 30−40% of the total land cover (Andren 1994; Fahrig 2001). The results showed that habitat connectivity was also a critical factor that influences species abundance and functional group diversity, especially insectivorous birds, in the landscape with approximately 30% of forest cover (Table 2-2). This result is consistent with the findings of previous research indicating that insectivorous birds are particularly susceptible to both reduced patch size and decreased connectivity (e.g., Martensen et al. 2008). Furthermore, many forest bird species mainly feed on insects. Because species richness and abundance of insects are negatively influenced by forest fragmentation (Gonzalez et al. 1998), their diversity may increase with habitat connectivity. Thus, it is possible to assume that the abundance of insectivorous birds is also correlated with habitat connectivity. In addition, it has been suggested that a high level of connectivity may favor higher abundances of local populations and, therefore, may reduce the extinction risk of species (Haas 1995; Brooker et al. 1999). This indicates that creating new habitats or enhancing the connectivity among urban forest fragments in landscapes at or below the fragmentation threshold of 30−40% forest cover is potentially crucial for long-term species persistence.

It has been argued that domestic and feral cats have a direct negative effect on bird abundance through predation in urban areas (e.g., Crooks and Soulé 1999). In this study, however, the presence of cats showed no negative relation with species abundance; rather, a positive association with the abundances of all forest birds and insectivores was found. A plausible explanation for this result is that cats prefer high–quality habitat, which can provide safe shelters against predators (i.e., human and dogs) and support the higher numbers of small mammals and birds. Furthermore, some studies suggest that small mammals may be more preferred

prey items for cats, with relatively few birds being eaten (e.g., Barratt 1997, 1998).

Large rivers are generally considered impediments to dispersal for forest birds (Hayes and Sewlal 2004). The results showed that the large river in this study, which may act as a barrier, was only associated with the abundance of edge species. Although species with low dispersal ability could never move freely and disperse across river barriers, they may disperse and colonize urban forest fragments from adjacent or distant large forests within two landscapes separated by the river (Fig. 2-2). Furthermore, the difference in the abundance of edge species between the north and the south sites may be due to the difference in the amount of edge in the surrounding landscape and a further work is required to identify such relationship.

Urban forests offer many essential ecological services, including the habitat provision for birds and other wildlife species, as well as benefits to humans (Millenium Ecosystem Assessment 2005). Thus, the conservation of urban forests is vital to sustain healthy ecosystems. Birds, which are located high in the food chain, could thereby serve as reasonable surrogates for assessing urban forest condition and biodiversity. The results elucidate important local and landscape factors affecting functional bird diversity. Overall, this study showed that the diversity of bird species in an urban-fragmented landscape is mainly influenced by patch size and human disturbance and, to a lesser extent, by vegetation complexity and connectivity. Local improvements in urban habitat structure—through increased patch area, reduced human disturbance, and increased vegetation complexity—could positively contribute to local species diversity. Moreover, preserving and promoting connectivity may enhance regional bird biodiversity, and such management strategies require the identification of crucial regions and gaps for connectivity between existing urban fragments so as to establish new habitats and corridors (i.e., revegetation) with more effective, ecological functions.

CHAPTER 3: Connectivity of protected forest area network as related to forest mammal roadkills

3.1 Introduction

Habitat loss and fragmentation due to human encroachment continue to threaten wildlife populations and diversity (Bascompte and Solé 1996; Forman and Alexander 1998; McKinney 2006; Devictor et al. 2007). In particular, roads linking man-made infrastructure systems and other human developments have significant adverse impacts on wild animals through not only disconnecting them from essential habitats but also restricting their physical movements (Forman and Alexander 1998). Because roads play a significant role in injuring and killing animals by vehicle collisions, it is directly connected to a critical matter for wildlife survival (Trombulak and Frissell 2000).

The mortality of animals due to vehicle collisions is well documented (Bruinderink and Hazebroek 1996), and there are a number of studies on causes of roadkill. For instance, Hussain et al. (2007) reported that traffic volume was highly correlated with animal road mortality, while Gunther et al. (1998) implicated speed as the major reason for animal–vehicle collisions. On the other hand, little empirical research has been done in investigating how landscape structure and configuration surrounding roads affect the mortality and survival of animals (e.g., Clevenger et al. 2003). Nevertheless, through some related studies, it is found that roadkill frequency is not a random consequence but spatial-dependent (e.g., Child 1998; Hubbard et al. 2000; Clevenger et al. 2001; Joyce and Mahoney 2001; Clevenger et al. 2003; Danks and Porter 2010). Moreover, it is known that despite the efforts to restore landscape connectivity across roads with some wildlife crossing structures (Clevenger 2005), many wildlife roadkills still occur throughout

the country (KNPS 2009).

Empirical data from field studies, however, are insufficient to provide guidelines for connecting habitats across roads. In conducting such empirical studies, landscape spatial patterns are important factors that need to be considered for the distribution and the abundance of roadkills (Forman and Alexander 1998), as available habitat types and configuration of those habitats are critical factors for the existence of wildlife. In other words, it is imperative that the relationships between roadkill patterns and landscape structure, especially connectivity, should first be thoroughly examined.

It is unknown whether protected area networks fragmented by roads are capable to sustain multiple species. Because species have different habitat area requirements and different movement abilities, the habitats linked by road-crossing structures that are perceived as well-connected for one species or a group of species may not be suitable for another species (Minor and Lookingbill 2010). Hence, explanatory factors of wildlife road-kills may vary widely between species and taxa. Some studies, however, have addressed road mortality in various mammals groups (e.g., Seiler et al. 2004). For example, there have been few studies in relation to the influence of road and landscape features on causing small mammal roadkills (e.g., Oxley et al. 1974; Groot Bruinderink and Hazebroek 1996; Bissonette and Kassar 2008), while most previous studies largely concentrated on identifying important variables for large mammal roadkills (e.g., Philcox et al. 1999; Clevenger et al. 2003; Hussain et al. 2007; Pereira et al. 2011).

The road density of greater than 0.6 km/km^2 is known to decrease the persistence of wildlife populations (Switalski 2006). The road density in South Korea was 1.05 km/km^2 in 2009 (World Bank 2010). Thus, Korea is not an exception when discussing the growing concern about mitigation, limitation, and prevention against animal-vehicle collisions.

This study evaluated the spatial distribution of protected area networks in South Korea, and assessed the relationship between landscape connectivity and roadkill distribution of forest mammals with varying resource demands and life histories. In addition, the impact of potential barriers, particularly major roads and rivers, on the connectivity of protected area network was also assessed. Graph theoretical methods were used to investigate whether the connectivity of protected area network are correlated to the roadkill distributions of different groups of species and whether protected area networks are sufficient to allow movements and dispersals of various species. Graph theory is an efficient tool for measuring physical relationships among landscape elements (i.e., structural connectivity) and how these relations influence species movements within a landscape (i.e., functional connectivity) (Calabrese and Fagan 2004; Urban et al. 2009). Functional connectivity for various mammals was examined, using the data on their habitat area requirements, the movement abilities, and the distribution and abundance of roadkill. The general hypothesis of the research in this section is that the abundance of roadkill is dependent on the connectivity of protected area networks.

3.2 Materials and methods

The study area is the southern part of the Korean Peninsula (Fig. 3-1), which lies between latitudes 33° and 39°N, and longitudes 124° and 131°E, and covers 96,390 km^2 (MLTM 2012). Approximately 64% of the land, mostly in the north and east, is covered by mountains (Korea Forest Service 2012). Data collected for the study were the records of the distribution and abundance of road-killed forest mammals on 16 roads between 1.2 and 20.0 km in length from National Institute of Biological Resources (NIBR 2012) (Fig. 3-1). These surveys were periodically conducted at the fixed road intervals every year from 2006 to

2012 by national park managers. In analyzing the findings, this research focused on 19 forest mammal species (Table 3-1).

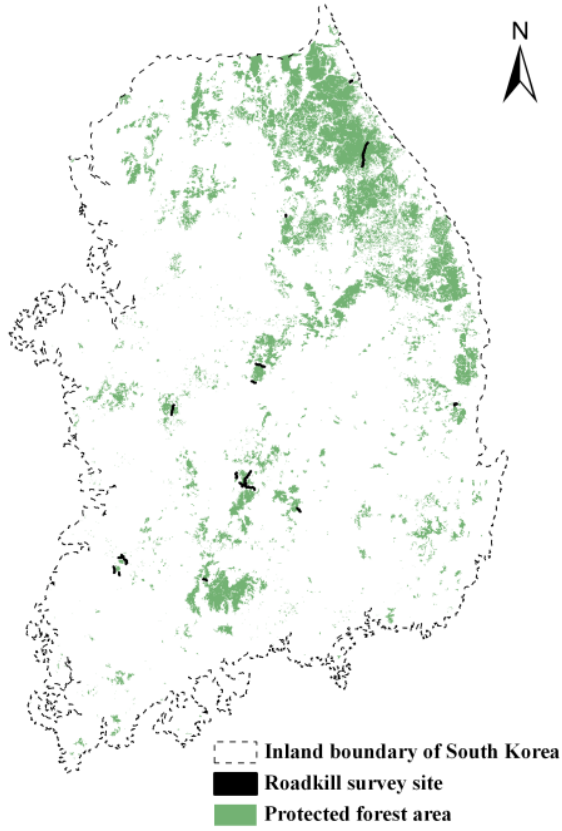

Fig. 3-1. Roadkill survey sites (n=16) (KNPS 2009) and protected forest areas.

Spatial data and information about the protected forest areas in South Korea were obtained from the Ministry of Environment (ME 2007). They include the highest level of biodiversity and are under the first grade of protection. The two main inputs for connectivity modeling were the dispersal distance and the home

range area of the 19 mammals. The relationship between these two variables was searched based on previous studies (see Table 3-1). These data were plotted and the least-square regression line was fitted to choose scales of analysis (Fig. 3-2). Three positions along the regression line were identified to represent three distinct scales: small scale, for mammals with short dispersal distances (300 m) and small home ranges (1 ha); intermediate scale, for mammals with intermediate dispersal distances (1,500 m) and intermediate home ranges (10 ha); and large scale, for mammals with large dispersal distances (10 km) and large home ranges (100 ha). The round numbers were employed (e.g., 300 m dispersal distance and 1 ha home range) to define more general relations. The three groups approximately corresponded to small-, intermediate-, and large-bodied species, and these groups are referred as small mammals, intermediate mammals, and large mammals in the present work. For analysis purposes, except large mammals, the study calculated the average number of road-killed individuals of each group per year within each survey road site as dependent variables. In case of large mammals, because the number of the observed roadkills of large mammals during the seven years was too low, the total number of road-killed individuals was chosen.

Table 3-1. Forest mammal species included in the study, and the number of road-killed mammals on 16 roads (a total distance of 102.5 km) from 2006 to 2012. Species were assigned to different mammal groups based on their mean home range and dispersal distance, estimated from or reported in published papers.

Common name	Species name	# of roadkill obs.	Home range size (km^2)	Dispersal distance (km)	Mammal group	Reference
Amur Goral	*Naemorhedus caudatus*	0	1.380	15.89	Large	Lee et al. 2011
Asian Badger	*Meles leucurus*	6	1.000	5.50	Large	NIER 2009
Eurasian Red Squirrel	*Sciurus vulgaris*	59	0.060	0.15	Small	Lurz et al. 2000
Hedgehog	*Erinaceus amurensis*	11	0.230	2.00	Intermediate	Morris 1988
Korean Hare	*Lepus coreanus*	42	0.210	1.62	Intermediate	Ruhe and Hohmann 2004; Bray et al. 2007
Korean Wood mouse	*Apodemus speciosus*	13	0.002	0.10	Small	Ko et al. 2011
Least Weasel	*Mustela nivalis*	0	0.010	0.50	Small	Sheffield and King 1994
Leopard Cat	*Prionailurus bengalensis*	13	3.700	7.00	Large	Choi and Park 2009
Lesser Japanese Mole	*Mogera wogura*	18	0.060	1.10	Intermediate	Loy et al. 1992
Raccoon Dog	*Nyctereutes procyonoides*	82	0.800	2.40	Intermediate	Woo 2010
Red-backed Vole	*Clethrionomys rufocanus*	7	0.001	0.10	Small	Lee 2011
Roe Deer	*Capreolus pygargus*	3	0.054	2.00	Intermediate	Yoon 2003
Siberian Chipmunk	*Tamias sibiricus*	482	0.008	0.20	Small	Ko et al. 2011
Siberian Flying Squirrel	*Pteromys volans*	1	0.340	2.15	Intermediate	Hanski et al. 2000
Siberian Weasel	*Mustela sibirica*	44	0.015	0.50	Small	Sasaki and Ono 1994
Striped Field Mouse	*Apodemus agrarius*	2	0.006	0.10	Small	Lee 2011
Ussuri White-toothed Shrew	*Crocidura lasiura*	8	0.002	0.10	Small	Lee 2011
Water Deer	*Hydropotes inermis*	49	0.340	0.78	Intermediate	Kim 2011
Wild Boar	*Sus scrofa*	1	5.130	10.60	Large	Choi et al. 2006

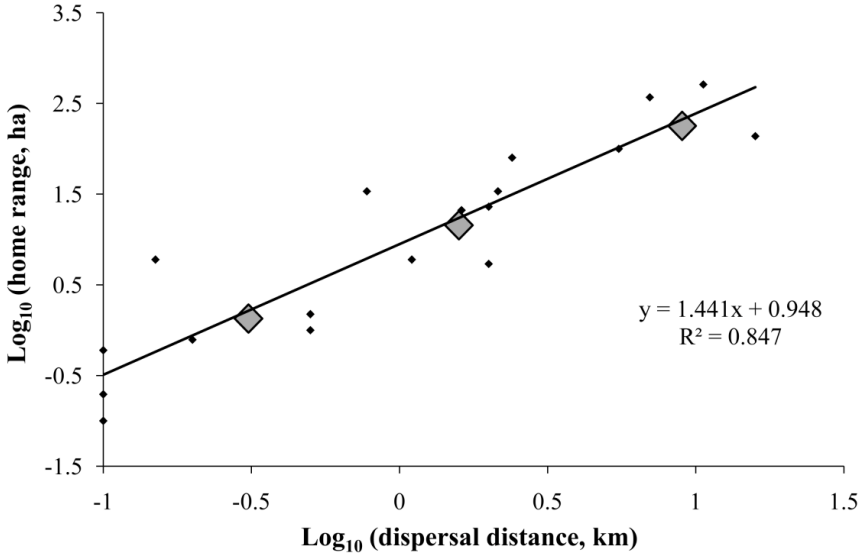

Fig. 3-2. Relationship between dispersal distance and home range size of mammals (small diamonds, individual mammal species; line and equation, linear least square regression; large diamonds from left to right, small, intermediate, and large mammal groups used to analyze the relationship between the connectivity of protected-area network and the abundance of road-killed forest mammals).

Forest areas (i.e., patches) that met the minimum home range requirements of each mammal group were included (1, 10, and 100 ha for small, intermediate, and large mammals, respectively). Therefore, the patches included in the network of large mammal protected areas were a subset of patches in the network of intermediate mammal protected areas, which were again a subset of patches in the network of small mammal protected areas. Forest patches were considered being connected if they were as close as or closer than the maximum dispersal distance of the mammals in the group (300 m for small mammals, 1.5 km for intermediate mammals, and 10 km for large mammals). The Euclidean distance

between patches was measured from the edge of one patch to the edge of the other.

A graph theoretical approach was employed for measuring and visualizing network connectivity as an independent variable (Urban and Keitt 2001). Graph theory allows broad applications in a wide range of disciplines including mathematics, social science, computer science, and landscape ecology (Hayes 2000a, b). In the methodological approach, a graph is a set of nodes (i.e., discrete habitat patches) connected by links (i.e., movement of organisms) (Minor and Urban 2008). Lines between all connected patches were drawn using the Graphab 1.0 (Foltête et al. 2012). The level of inter-patch connectivity was then quantified as *area-weighted flux* (AWF) (i.e., amount of dispersal or movements) (Minor and Urban 2007; Laita et al. 2011). Flux from a donor patch i to a recipient patch j is calculated as the dispersal probability between two patches (P_{ij}) multiplied by the area size (a_i) of the donor patch ($\text{Flux}_{ij} = a_i \times P_{ij}$). Probability ($P_{ij}$) expresses the probabilities that an individual in the donor patch will disperse to the recipient patch. It can be approximated as negative exponential decay:

$$P_{ij} = \mathrm{e}^{-k \cdot d_{ij}}$$

Where k is a constant and d_{ij} is the distance between the patches. A dispersal probability of 0.05 was defined to correspond to the maximum dispersal distance of the mammals in the group (i.e., 300 m, 1.5 km, and 10 km threshold distance, if exceeded a pair of patches have no link). Here, AWF was simplified by averaging the two directions, yielding an area-weighted flux (w_{ij}) for each pair of nodes. High flux between patches indicates a large number of dispersal events. Thus, road that crosses a certain area with a higher degree of flux between surrounding patches may have a high probability of roadkill. The connectivity (i.e., amount of flux) of links that intersected with each road site was summed.

Also, road features and other multiple factors were computed, in relation

to the spatial patterns of roadkill and species requirements (Hussain et al. 2007; Danks and Porter 2010): (1) road length; (2) traffic volume; (3) distance to nearest patch larger than minimum home range requirement of each group of mammals; (4) distance to stream; (5) elevation; and (6) slope. At each road site, the traffic volumes were averaged (vehicles / road length (km)), of which data were obtained from aerial photographs including Google Earth (Spot image, dated from April 2007), DAUM imagery of Daum Communications Corp. (0.5 m resolution, dated from May 2011), and NHN imagery of Next Human Network Corp. (0.5 m resolution, dated from August 2008). Elevation and slope were derived from a 30 m digital elevation model (DEM).

Spatial autocorrelation in the abundance of each group of road-killed mammals was first examined using a Moran's I at ten Euclidean distance classes from 5 km to 50 km. The Moran's I test was performed with the package ape in R (Paradis et al. 2004). Three separate generalized linear models (GLMs) were formulated, using a log link function assuming a Poisson distribution, to explore the influence of network connectivity intersected with road (i.e., flux measures) based on dispersal distances and home range areas of each group of mammals, road features, and topographic factors on the abundance of road-killed mammals of each group. Before executing multivariate regressions, multicollinearity among independent variables was examined by performing Pearson's correlations. The results showed that no variables were highly correlated (i.e., $|r| < 0.7$).

A model averaging approach was used based on information criterion for model selection (Burnham and Anderson 2002). First, all models were ranked according to the corrected Akaike Information Criterion (AICc) using the MuMIn package in R (Barton 2011). Then, variables included in the most parsimonious models that had △AICc values below 4 were considered, by averaging their estimated coefficients and standard errors weighted by AICc of each model

(Burnham and Anderson 2002). Finally, model–averaged parameter estimates and unconditional standard errors were presented for each variable as well as the best model with the lowest AICc value. The relative importance of each independent variable was also estimated by summing the AICc weights of the parsimonious models in which that variable appeared. All independent factors were log-transformed (log[x + 1]) so as to improve normality.

In order to test the single focal species approach to protected area network design, it was also examined whether the connectivity of protected area networks for large mammals was related to abundance of road–killed small mammals through using the model averaging method described above. Instead of the level of connectivity scaled for small mammals, connectivity variable estimated for large mammals was included, with other road and landscape variables, in order to explain variation in the response variable abundance of road–killed small mammals.

For examining the potential barrier effects of roads and rivers on protected area networks of each mammal group, all protected forest patches that were separated by roads and rivers were regarded as disconnected. Typically, a road with higher traffic levels (e.g., ≥80 km/h (i.e., ≥50 mi/h)) comparatively leads to more roadkills than lower-volume and lower-speed roads (Gunther et al. 1998). Thus, the roads with a speed limit higher than 80 km/h were chosen. Large rivers with a width over 100 m were also selected, as they act as a natural barrier against forest mammals. Prior to this, network connectivity of each mammal group with both the absence and presence of these barrier effects was graphically presented. Two connectivity metrics, area-weighted flux and probability of connectivity (PC) were applied. Area-weighted flux accounts for the local flow of organisms at the level of the local neighborhood. PC accounts for not only the local neighborhood connectivity, but also the movements of organisms beyond the scale of the local neighborhood (Saura and Pascual-Hortal 2007). Then, Wilcoxon rank-sum tests

were first employed to compare the initial measure of total area-weighted flux to a second estimate of connectivity that incorporated roads and rivers.

The probability of connectivity (PC) is computed as:

$$\mathrm{PC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_L^2}$$

where n is the total number of patches, a_i and a_j are the areas of patches i and j, and A_L is the total landscape area. p_{ij}^{*} is defined as the maximum product probability of all possible paths between the patches i and j. The product probability of a path is the product of all the p_{ij} (link weights) included in the path. The p_{ij} (dispersal probability) is generally given by a negative exponential as a function of inter-patch edge-to-edge distance (Urban and Keitt 2001). When $i = j$, the p_{ij}^{*} equals 1. PC is defined as the probability that two organisms which were randomly placed in a landscape fall into habitat areas that are reachable from each other (i.e., interconnected), given a set of habitat nodes and links between them (Saura and Pascual-Hortal 2007). It ranges from 0 to 1 and reaches unity when the landscape is entirely covered by a given habitat type. Also, PC is regarded as a habitat availability index because it integrates topological properties of the habitat network with habitat area attributes (Saura and Pascual-Hortal 2007). The PC index may be an appropriate metric to study overall flows of organisms irrespectively of their origin (Bodin and Saura 2010). A dispersal probability of 0.05 was defined to correspond to the maximum dispersal distance of each group of mammals (i.e., the cut-off distance, if exceeded a patch pair have no link). Conefor Sensinode 2.6 was used for measuring PC values with and without the effect of potential barriers on dispersal movements of forest mammals (Saura and Torné 2009), and percent decrease in the PC values for each mammal group was calculated.

3.3 Results

A total of 841 individual kills (ca. 1.17 per km of road per year) consisting of 17 species of forest mammals were recorded (Table 3-1). The result showed greater mortality for small (n=615, 73.1%) and intermediate (n=206, 24.5%) mammals than large (n=20, 2.4%) mammals. Siberian chipmunk (n=482) was the major victim among the small mammals. In the intermediate mammals most killed was raccoon dog (n=82). Among the large mammals leopard cat was the common one (n=13). The Moran's I test for the abundance of each group of road-killed mammals showed no evidence of spatial autocorrelation ($p > 0.05$) across all distance classes.

On the basis of a △AICc <4, three models were equivalent in terms of describing the abundance of small road-killed mammals (Table 3-2), and they explained nearly every proportion of variance (ca. 99%). Three significant variables included in the best model were connectivity, road length, and distance to patch >1ha, all with positive signs. According to the results, these three were the most important variables predicting small mammal roadkills. For intermediate mammals, 13 models had a △AICc <4 and accounted for similar proportions of variance (ca. 68%) (Table 3-2). Connectivity was the strongest predictor in intermediate mammal models, with a positive sign. Finally, 14 models were equivalent in terms of explaining the variation of large mammal roadkills, all of which explain similar proportions of variance (67%). Again, connectivity, which had a positive influence on the abundance of roadkill, was the most important variable in the large mammal models. However, connectivity scaled for large mammals had no influence on the abundance of road-killed small mammals ($p > 0.05$; data not shown).

The protected area network seemed to be relatively well-connected for

large mammals, but not for intermediate and small mammals without considering the barrier effects (Fig. 3-3). Wilcoxon rank-sum tests showed a non-significant change in local neighborhood connectivity for each mammal group when potential barriers were included (small mammals, $\chi^2 < 0.001$, $p = 0.976$; intermediate mammals, $\chi^2 = 0.002$, $p = 0.967$; large mammals, $\chi^2 = 1.474$, $p = 0.225$), but they indicated that the mostly affected mammal group by potential barriers was large mammals. The percent decrease in PC connectivity for the intermediate and large mammals were 25.4 and 24.1%, respectively, twice as high as that of the small mammals (11.3%).

Table 3-2. Regression coefficients ±SE of connectivity scaled for each mammal group, road features, habitat proximity indices, and topographic variables and adjusted R^2 values of the generalized linear models with Poisson error obtained for the abundance of road-killed small, intermediate, and large mammals. Akaike's Information Criterion (AICc) and AICc weights (w_i), respectively, were used to rank models and to estimate relative importance (sum of AICc weights over the most parsimonious models (△AICc <4) in which the variable appeared) of the variables. The number of models averaged in each case is presented in parentheses. An asterisk (*) indicates the variables for which its effect on the model was significant at p <0.05.

Model	Connectivity	Road feature		Distance to nearest		Topographic factor		AICc	w_i	Adj R^2
		Length	Traffic volume	Patch	Stream	Elevation	Slope			
Small mammals										
Relative importance	1.00	1.00		1.00	0.16	0.13				
Best	0.47±0.12*	3.61±0.72*		0.58±0.18*				70.39	0.71	0.99
Average (3 models)	0.46±0.12*	3.58±0.79*		0.56±0.18*	-0.13±0.11	-0.63±0.62		72.50	0.33	0.99
Intermediate Mammals										
Relative importance	0.85	0.29	0.33	0.22	0.05	0.10	0.16			
Best	0.65±0.15*							54.17	0.22	0.64
Average (13 models)	0.57±0.20*	1.66±1.01	1.30±0.86	-0.28±0.19	0.01±0.12	-0.82±0.82	-1.10±1.09	56.61	0.08	0.68
Large mammals										
Relative importance	0.67	0.44	0.24	0.07	0.53	0.04	0.04			
Best	0.65±0.20*				-0.35±0.19			41.28	0.22	0.71
Average (14 models)	0.66±0.26*	2.35±1.18	1.46±1.18	0.06±0.27	-0.34±0.20	-0.21±1.12	-0.17±1.30	43.92	0.07	0.67

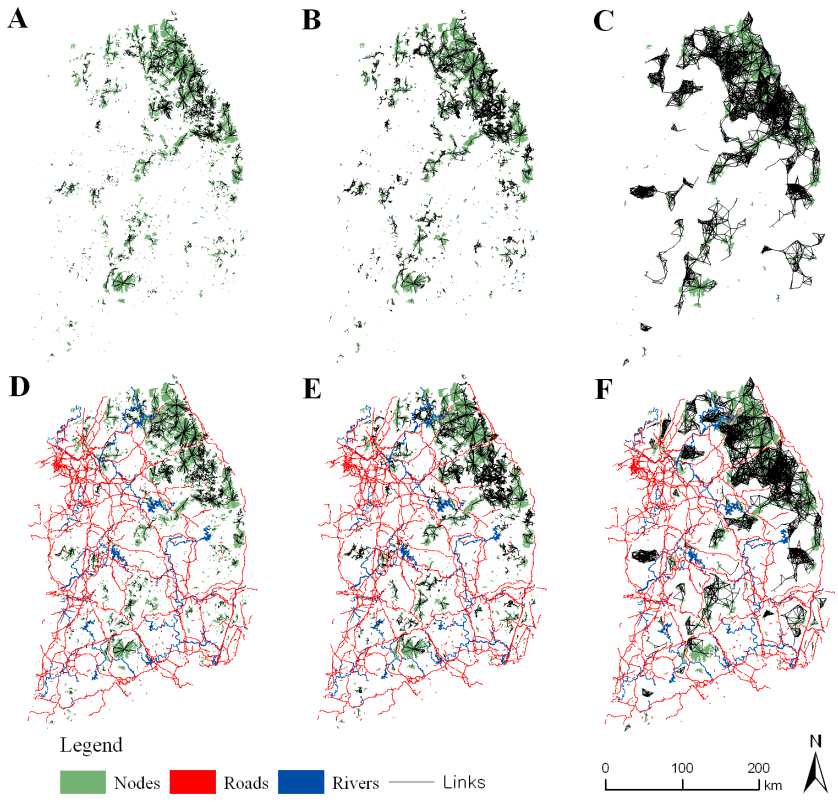

Fig. 3-3. Network connectivity of each mammal group with both the absence (A, small; B, intermediate; C, large mammals) and presence (D, small; E, intermediate; F, large mammals) of the barrier effects.

3.4 Discussion and conclusions

The purpose of this study was to use the forest mammalian roadkill survey data to investigate how roadkill abundance is influenced by the connectivity of the protected forest area networks, road characteristics, and landscape features. Because species have different habitat area requirements and dispersal abilities, this study explored three different groups of road-killed forest mammals, including small, intermediate, and large ones. The result showed that small mammals are most likely to become road-killed. Also, in all three cases, the number of roadkill increased with the increase of network connectivity levels, showing roadkills occur mainly on roads that intersect movement routes with high connectivity. Thus, the finding highlights the importance of maintaining connectivity at multiple scales. In addition, large mammals are likely to be more affected by potential movement barriers than small mammals, because of their tendency to intersect more with barriers, owing to their long-distance movements (Minor and Lookingbill 2010). Overall, the results indicate that different connectivity conservation strategies should be implemented for different groups of species to increase the likelihood of persistence of forest mammals.

As stated earlier, roadkill survey data showed that small mammals are the most frequently killed mammal group on roads. Among the small mammals, Siberian chipmunks were most commonly killed, followed by Eurasian red squirrels. This may be because these small rodents are diurnal species with a high possibility to cross roads during the daytime when there are relatively high traffic volumes and speeds. Because of the reduction of driver visibility in the poor light and of dazzled and bemused nocturnal animals due to the bright vehicle headlights, it is known that nocturnal mammals are more likely to be killed than diurnal species (Bullock et al. 2011). However, the overlapping time periods between

primary movement times of species and high traffic volumes could lead to an increase in roadkill rates of other species (Haikonen and Summala 2001). Among the intermediate mammals, raccoon dog was the most common road-killed animal. When comparing with other intermediate mammals, high roadkill rates for raccoon dogs seem to be associated with their long distance movement and the probable tendency to use linear features such as roads and gutters if they are available (Saeki et al. 2007). Meanwhile, large mammals such as Amur goral and wild boar had rare rates of roadkill, because they are thought as specialist species of interior habitats that avoid approaching roads verging their habitats and, therefore, avoid crossing roads (Choi and Park 2005; Choi 2007).

The level of connectivity of protected area networks scaled for each mammal group appeared to have the greatest influences on the roadkill abundance of each mammal group. This result showed that roadkill hotspots occurred mainly on the roads intersecting the areas with high rates of inter-patch connectivity. Moreover, this finding highlights the importance of maintaining the inter-patch connectivity (i.e., improving the permeability of roads) at multiple scales. In other words, a single focal species (typically a large carnivore presumed as an umbrella species) approach may not be appropriate for designing and managing multi-species protected area networks (Minor and Lookingbill 2010). Some studies also reported that optimized movements of large carnivores do not necessarily represent those of other species across a landscape (e.g., Beier et al. 2009). The present research provides further evidence that the level of connectivity for large mammals is not associated with the abundance of road-killed small mammals, implying that smaller mammals' movements may not be predicted by the level of connectivity for large mammals. That is to say that the movement of large mammals is feasible among protected areas, but it is difficult to expect the same function of large protected areas for small mammals. The distance between large protected areas is

not closely connected with one another nor do they necessarily have smaller reserves between the larger areas, which can function as stepping stones that facilitate the movement and dispersal of species. Overall, it can be concluded that separate connectivity measurements of specific groups of species, rather than a focal species, are necessary for protected areas including multi-species networks (Minor and Lookingbill 2010).

While connectivity was an influential variable for all mammal groups, load length was the only variable positively related to the vehicle collisions of small mammals, indicating the road itself creates a barrier to the movements of small mammals (Rico et al. 2007). The distance to the nearest patch was also a significant positive predictor of small mammal roadkills. This result is presumably because of a negative correlation between proximity to road and habitat quality (Fahrig and Rytwinski 2009), combined with more immigration events from the protected areas with a high productivity. In this regard, within the vicinity of roads, high-quality (undisturbed) habitats that are relatively far from the roads may support more productive populations of small mammals and could act as dispersal sources. In the process of frequent immigration from high-quality protected areas to other desirable areas, there is a high probability for the small mammals to cross the intersecting roads, which sometimes may lead to an increase in their roadkill rates.

Traffic volume and speed are suggested to be the most influential variables for mammalian roadkills in several related studies (e.g., Inbar and Mayer 1999; Trombulak and Frissell 2000; Joyce and Mahoney 2001). However, traffic volume was not an important factor for the forest mammal vehicle collisions in the present research, presumably because of the fact that investigated roads pass through national parks in Korea. In general, there are very low road traffic volumes at night on roads around the national parks, and most roads are small with

comparatively low traffic volumes.

The roadkill data used in this study was based on the official animal carcass count survey, which has been continuously conducted by the Korea national park service. Some studies have suggested several issues regarding animal carcass count surveys. For example, the time of carcass persistence, which is defined as the time each road-killed animal remained on the road, has been considered an important factor that can induce bias in road mortality estimates (e.g., Santos et al. 2011). The carcass persistence of larger mammals is assumed to be longer than that of small ones, which indicates the importance of the frequent monitoring surveys so as to ensure the estimates of various sized species including small animals. In other words, the frequency of a roadkill survey is another contributing factor to the reliability of carcass reports (Santos et al. 2011). Although the count survey used in the study is being conducted at least once a week on a car vehicle with the lowest speed on roads, it is still required to make more efforts to collect more accurate and detailed data on carcass. In this regard, some studies recommend alternative methods, such as a count survey on foot on a daily basis, while acknowledging the difficulty derived from time and manpower (e.g., Enge and Wood 2002; Slater 2002; Santos et al. 2011).

The roadkill rate may not be related to population density (Hobday and Minstrell 2008), but may be associated with population size (Seiler 2001). In other words, the increase in the number of roadkill may be linked to wildlife abundance. Moreover, some studies reported that the number of roadkill varied temporally due to the seasonal variation in activity patterns and abundance of wildlife (e.g., Conard and Gipson 2006). Although the present study did not reflect the relationship between population size and roadkill frequency, the understanding of impacts of local and landscape factors on such relationship is an important research subject that needs to be further investigated, possibly with more accurate seasonal

and spatial estimates of roadkill and population size.

In the study area, a well-connected network of protected areas was found for large mammals, whereas the network for the intermediate and small ones was not well-connected (Fig. 3-3). However, the network connectivity for forest mammals, especially with large home ranges and distant movements, was greatly reduced when potential barriers were included in the network analysis. These results suggest that it is essential to consider creating additional habitat patches that can connect the existing core habitats for the conservation of small mammals, while large mammals' conservation would benefit from securing movement paths and corridors that crosses barriers such as roads and rivers.

Roads are indeed barriers to resources and migration for many specialized forest animals as well as for the others which are attracted to the roads, thereby risk being killed (Forman and Alexander 1998; Fahrig and Rytwinski 2009). It is evident that the roads with high roadkill frequency usually pass through the areas with the high existing or potential habitat connectivity for forest mammals and other species. Roadkill monitoring may identify such areas, but the identification of roads that intersect high inter-patch connectivity is another precise and efficient approach to plan the permeability of roads and, thus, to maintain the metapopulations of the mammals. By establishing the relationship between roadkill patterns and connectivity of protected area networks at multi-scales and then by identifying areas of high roadkill risk, plausible recommendations for roadkill mitigation can be made as follows: (1) to construct fences on roads and wildlife crossing structures based on species- or group-specific preferences, such as overpasses and underpasses, and (2) to notify vehicle drivers of wildlife crossings with wildlife signage to reduce their speeds.

This study demonstrated that inter-patch connectivity played an important role in determining the roadkill locations and the roadkill rates of all three different

mammal groups. Because the occurrence of roadkills may spatially and temporally differ depending on local environmental conditions and landscape context, more detailed research data are necessary to verify the relationship between the roadkill levels and the degree of functional connectivity. Further research is also required to select suitable locations for wildlife crossing structures based on multi-scale connectivity models. The rapid development of roads and subsequent continuous decrease in connectivity will be a consistent major threat to long-term survival of mammal populations.

CHAPTER 4: Habitat network and population genetic structure of a threatened tree *Kalopanax septemlobus* in South Korea

4.1 Introduction

Habitat fragmentation caused by urbanization represents a major threat to biodiversity (McKinney 2002), as small and isolated populations frequently undergo loss of genetic diversity, which eventually increase extinction risk (Noël et al. 2007). In fragmented landscapes, spatially structured populations (i.e., metapopulations) may only persist regionally, which is strongly related to landscape connectivity and dispersal process (Hanski and Ovaskainen 2003). In addition, climate change is also predicted to become one of the major drivers of changes in biodiversity and ecosystem, and its possible effects are receiving worldwide attention (Sala et al. 2000; Duraiappah et al. 2005). Indications for impacts of climate change have already been found in many species over a wide taxonomic range (Parmesan and Yohe 2003; Nussey et al. 2005; Parmesan 2006). Such impacts may be reinforced by combined effects of climate change and habitat fragmentation, which lead to species range shifts and reduction in landscape connectivity, respectively (Honnay et al. 2002; Opdam and Wascher 2004).

Although some species may have the ability to disperse to new habitats as vegetation shifts, the unprecedented speed and scale of projected climatic changes may limit their movement and distribution (Schloss et al. 2012). Thus, understanding species' range-shift capacities has important conservation implications for predictions of future extinction risk and distribution changes (Angert et al. 2011). More importantly, an effective adaptation strategy may be preserving and restoring landscape connectivity for long-term persistence of

ecological processes, such as gene flow (Rosenberg et al. 1997; Templeton et al. 2001; Crooks and Sanjayan 2006).

Landscape connectivity is defined as the degree to which the landscape facilitates or disturbs movement, dispersal, and gene flow among resources patches (Taylor et al. 1993). Estimating the amount of interaction between patches linked by dispersal and gene flow (i.e., functional connectivity) may be a feasible way to evaluate species persistence in response to climate change (Urban and Keitt 2001). Especially for plants, gene flow by seed and pollen movement among different populations plays an important role in the spread of adaptive traits, which may help species better adapt to climate change (Slatkin 1987; Templeton et al. 2001; Sexton et al. 2011). However, due to the difficulty in directly detecting and quantifying these migration events at the landscape level (Sork and Smouse 2006), understanding how landscape features affect species gene flow and shape population structure is a challenging task in changing environments.

Recently, landscape genetics, an integration of landscape ecology and population genetics, represents a conceptual framework for advanced estimation of gene flow with landscape connectivity (Manel et al. 2003; Galpern et al. 2012). In landscape ecology, connectivity is often analyzed by graph-theoretical methods with minimal data inputs, which show promise for providing functional and ecologically-relevant measures of landscape structure and process (Calabrese and Fagan 2004; Minor et al. 2009; Urban et al. 2009; Galpern et al. 2011). In molecular genetics, various statistical approaches using highly-polymorphic molecular markers provide the potential to accurately identify population genetic structure (Fujimori et al. 2006a). Therefore, graph-based landscape modeling combined with empirical data on population genetic structure is an effective approach for assessing functional connectivity (Fall et al. 2007; Galpern et al. 2012; Scheepens et al. 2012).

Although global warming is already beginning to affect regional climate system (Jung et al. 2002; Boo et al. 2004) and to cause range shifts of terrestrial flora in South Korea (Allen et al. 2010), it is unknown whether existing biosphere reserves and semi-natural forests can maintain species and genetic diversity. In this regard, this study investigated the relationships between habitat connectivity and gene flow for a threatened tree *Kalopanax septemlobus* (Araliaceae). Natural populations of *K. septemlobus* have been severely disturbed and fragmented by illegal logging for timber, medicine, and edible/food (Chang et al. 2001; Kang 2003). Species distribution and graph-based connectivity modeling with a population genetic analysis were combined in order to explore ecological processes and propose management alternatives (Galpern et al. 2012). The primary objectives in this section were (1) to identify climatic and topographic factors associated with *K. septemlobus* distribution and predict their suitable habitat; and (2) to use network analysis to predict gene flow and genetic diversity in populations of *K. septemlobus*.

4.2 Materials and methods

4.2.1 Study area and focal species

The study area is the southern part of the Korean Peninsula and islands of South Korea (Fig. 4-1). This area lies between latitudes 33° and 39°N, and longitudes 124° and 131°E, and covers 100,148 km^2 (MLTM 2012). Approximately 64% of the land is covered by mountains, mostly in the north and east (Korea Forest Service 2012).

Kalopanax septemlobus is a hermaphroditic, deciduous tree species endemic to Northeast Asia (Ohashi 1994; Lee and Kang 2002). *K. septemlobus*

have widespread distributions, but typically sparse populations (e.g., 1.03 trees/ha; Sawada et al. 2006). It is the only species within one genus of the Araliaceae family, and can grow up to 30 m in height with a diameter at breast height (DBH) of 1.8 m (Lee 1988). It flowers from July to August in South Korea, and various insects, including honey-bees and flower flies, act as the main agents of pollination (Fujimori et al. 2006b). The fruits ripen in September and October, and attract frugivorous birds and squirrels that can disperse seeds away from the source trees (Iida and Nakashizuka 1998).

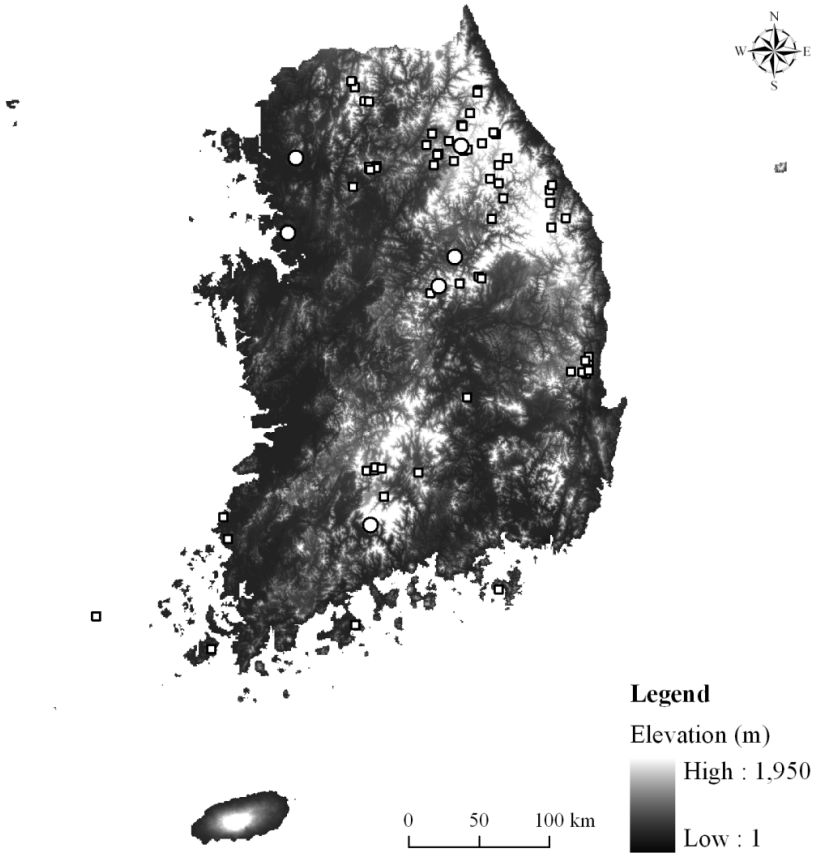

Fig. 4-1. Digital elevation model of the study area, with the presence locations of *Kalopanax septemlobus* (n=72) indicated as squares. Circles represent the genetic data sampling sites of six populations of *K. septemlobus*.

4.2.2 Habitat distribution modeling

Potential distribution of *K. septemlobus* was constructed by relating occurrence locations to bio-climatic and topographic variables, using a presence-

only machine learning modeling approach (Maxent) (Phillips et al. 2006). Occurrence records of *K. septemlobus* (n=72) were obtained from previously published studies (Lee et al. 2000; ME 2002; Kang 2003; Sakaguchi et al. 2012) (Fig. 4-1). The occurrence locations were separated by a minimum distance of 1 km to avoid spatial autocorrelation biases (Legendre et al. 2002). Four bioclimatic variables (mean annual temperature, mean diurnal range, annual precipitation of the warmest quarter and precipitation of the coldest quarter) at 1 km spatial resolution were obtained from the WorldClim database (Hijmans et al. 2005; http://www.worldclim.org/bioclim.htm). Four topographic variables, including slope and aspect (both in degrees), solar radiation, and topographic position index, were employed, derived from a 100 m digital elevation model. Potential solar radiation was calculated as the sum of direct, diffuse, and reflected radiation for one year based on terrain shading (Kumar et al. 1997). The topographic position index was generated using ArcView 3.3 with an extension by Jenness (2006). All variables were resampled to 100 m spatial resolution. Only variables contributing 1% or more to model were included in the final model. Multicollinearity was tested by examining Pearson's cross-correlations among all of the variables based on 10,000 randomly generated points within the study area. No variables were strongly correlated (i.e., $|r| < 0.7$).

Maxent modeling was performed using the default settings, with 1,000 instead of 500 iterations. Thirty model replicates were processed, with 70% of locations randomly selected each time to train the model and the remaining 30% used to test the model's predictions. The ENMtools 1.3 (Warren et al. 2010; Warren and Seifert 2011) was used to select the most parsimonious model based on the corrected Akaike's information criterion (AICc) scores (Burnham and Anderson 2002). Pixels with strong evidence of absence (occurrence probability <0.2) were removed from the analysis. Habitat patches were defined as contiguous pixels

using an eight-neighbor rule. For subsequent analyses, all patches <10 ha were excluded, which is considered to be the minimum stand size for the conservation of forest genetic resources (Guldager 1975; FAO 1985; Amaral and Yanchuk 2004).

4.2.3 Population genetic structure and diversity analysis

Individuals of six populations (n=96) in Korea were obtained, each typed at five microsatellite loci from Sakaguchi et al. 2012b (Fig. 4-1). Genetic differentiation among the populations, calculated as pairwise F_{ST} values (Weir and Cockerham 1984), was evaluated using FSTAT 2.9.3 (Goudet 1995). These values were linearized by using the formula $F_{ST}/(1-F_{ST})$ (Rousset 1997). In addition, in order to assess genetic diversity, observed heterozygosity (H_O) within each population was calculated using FSTAT 2.9.3 (Goudet 1995).

4.2.4 Habitat network analysis and isolation models

The network distance was calculated based on graph theory (Harary 1969), across every pair of populations to assess connectivity. In a habitat network, patches (i.e., nodes) are connected by links if dispersal or gene flow (i.e., functional inter-patch connection) is possible between them. Using a graph-theoretic approach, it is possible to analyze how patches are linked at various distance thresholds for species with different dispersal abilities (Laita et al. 2010) and to detect critical connectivity thresholds related to organism vagility (Keitt et al. 1997). Patch-based networks with connection distances ranging from 1 km to 100 km were created using Graphab 1.0 (Foltête et al. 2012), in order to identify gene flow related connectivity thresholds. Habitat networks were analyzed as undirected graphs (i.e., it was assumed that gene flow was equally likely to occur in either direction between pairs of habitat patches). Link weights were defined as edge-to-

edge Euclidean distances between patches. Each pairwise population of *K. septemlobus* was assigned a transformed network distance of Minor et al. (2009) based on network topology. If two populations were located in different habitat patches but in the same network component (i.e., groups of interconnected patches) at a distance threshold *t*, a network distance was calculated as follows:

$$\text{Network distance}_t = \frac{l_{ij}}{1 + l_{ij}}$$

where l_{ij} is the number of links in the shortest path between patch *i* and *j* associated with population *a* and *b* at a distance threshold *t*, respectively. It ranges from 0.5 to 1. If two populations were located in the same habitat patch, when $i = j$, a network distance equals 0. If two populations were located in different components, they were assigned a distance of 2. The shortest path length was calculated in R with the package igraph (Csardi and Nepusz 2006).

Conventional gene flow models based on point-to-point distance were also applied, including isolation-by-distance (IBD), least-cost path (LCP), and isolation-by-resistance (IBR) models (McRae and Beier 2007), for comparison with the patch-based network distance model. These isolation models assume that gene flow between populations may be reduced by geographic distance. In the IBD model, log-transformed Euclidean distances among populations were measured. In LCP model, log-transformed cost-weighted distances along the optimal routes connecting population pairs were measured. The inverse of occurrence probability of *K. septemlobus,* derived from Maxent modeling, was adopted as permeability values to calculate least-cost distances using PATHMATRIX software (Ray 2005). In the IBR model, resistance distances between population locations were calculated using Circuitscape version 3.5.8 (McRae 2006). The inverse of occurrence probability of *K. septemlobus* was also used as a resistance surface in

IBR analysis.

In order to analyze how habitat connectivity affects genetic diversity of *K. septemlobus* populations, two network centrality indices (degree and betweenness; Wasserman and Faust (1994)) were calculated as measures of patch importance in R with the package igraph. The degree centrality of a patch is the number of other patches linked to it (Harary 1969). The betweenness centrality is calculated as the proportion of the shortest paths between all pairs of patches which pass through the patch of interest (Freeman 1979). Degree and betweenness measure local and global centrality of patches in a habitat network, respectively (Estrada and Bodin 2008). Both measures depend on the threshold dispersal distance used to determine connectivity of patches. Centrality indices was log-transformed (log[x + 1]) to improve normality.

4.2.5 Gene flow and genetic diversity in relation to habitat connectivity

Mantel test (Mantel 1967) was employed to evaluate correlations between network distances at multiple scales and linearized F_{ST} and generated a Mantel correlogram (Legendre and Fortin 1989). The Mantel test was performed by the package vegan in R with 10,000 randomizations (Oksanen et al. 2008). Also, correlations between matrices of linearized F_{ST} and matrices of IBD, LCP, and resistance distances were calculated. To identify which model (IBD, LCP, IBR or Network) had the greatest support as the most significant predictor of population genetic differentiation, the study further compared the performance of network and isolation models using a partial Mantel test. The robust model should show a significant partial Mantel correlation with genetic distance after controlling for each of the three competing models, as well as the highest positive correlation with genetic distance (Cushman et al. 2006). To determine whether genetic diversity is

also related to habitat connectivity, Pearson correlations, between genetic diversity (i.e., observed heterozygosity) and degree and betweenness measured at the threshold distance that best predicted the gene flow, were calculated.

4.3 Results

The best model for predicting the *K. septemlobus* occurrence probability had a good fit ($AUC\text{-}_{train}$ = 0.89; $AUC\text{-}_{test}$ = 0.85). Among the eight variables, the most influential predictor was mean annual temperature, followed by slope. The relative contributions of variables in the model were as follows: (1) annual mean temperature (65.3%); (2) slope (16.8%); (3) precipitation of the warmest quarter (5.8%); (4) precipitation of the coldest quarter (4.5%); (5) mean diurnal range (2.4%); (6) aspect (2.3%); (7) solar radiation (1.6%); and (8) topographic position index (1.1%). At a mean temperature range over about 6 degrees Celsius, *K. septemlobus* negatively reacted to the annual mean temperature (data not shown). It responded to the slope in a v-shaped manner, having the lowest occurrence probability at approximately 5 degrees (data not shown). The potential distribution based on the model was similar to the actual species distribution (Fig. 4-2).

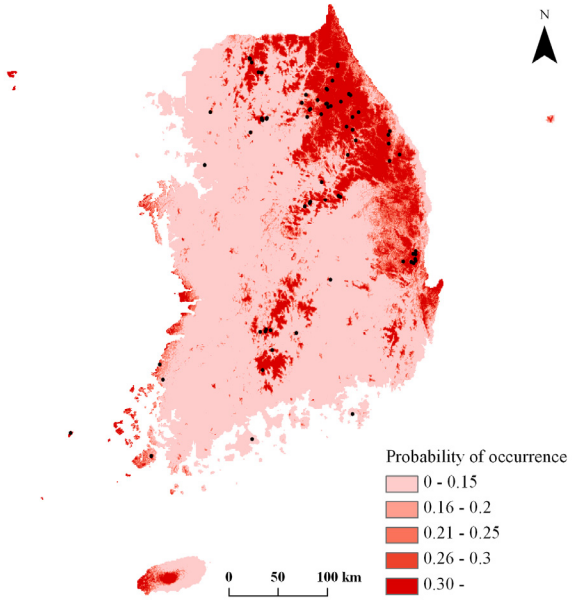

Fig. 4-2. Habitat suitability map for *K. septemlobus* based on the best Maxent model predictions. Distribution records of *K. septemlobus* are also marked with black dots.

The tests using Mantel correlograms showed significant positive correlations ($p < 0.05$) between genetic distance matrices and the matrices of network distances at scales ranging from 1 km to 30 km (Fig. 4-3). In addition, the genetic distance between population pairs was highly correlated with network distances calculated for the threshold distances 4–5 km (Mantel $r = 0.74$, $p < 0.01$; Fig. 4-4D). This is a range of scales at which the population genetic structure of *K. septemlobus* is strongly associated with habitat connectivity.

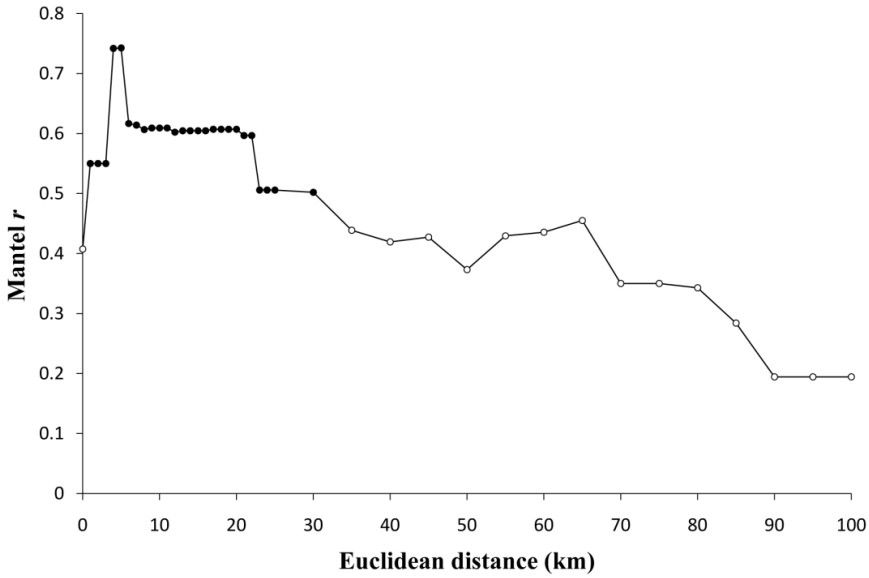

Fig. 4-3. Mantel correlograms between pairwise $F_{ST}/(1-F_{ST})$ values and network distances. Closed circles highlight significant Mantel test results (p <0.05).

Among the conventional gene flow models, LCP and IBR models exhibited a significant or near significant (i.e., $p < 0.1$) correlation with genetic distance (Mantel $r = 0.51$ and 0.57, respectively; Fig. 4-4). The partial correlations between LCP and IBR predictions and genetic distance were either significant or near significant ($r > 0.60$, $p < 0.062$) after controlling for IBD. In addition, there was no correlation between LCP prediction and genetic distance after controlling for IBR model (partial Mantel $r = 0.07$, $p = 0.40$).

A significant positive relationship between genetic distance and the network distance measured at the threshold distance of 5 km which best predicted the gene flow remained even after controlling for predictions of all competing models (partial Mantel $r > 0.58$, $p < 0.05$). This showed that network-based model of habitat connectivity better explained population genetic differentiation than IBD,

LCP, and IBR models did. The gene flow network of habitats was well connected at the 5 km maximum distance (Fig. 4-5). Finally, genetic diversity measured as the observed heterozygosity was positively correlated with both the degree and betweenness centrality based on the threshold distance of 5 km ($p < 0.05$; Fig. 4-6).

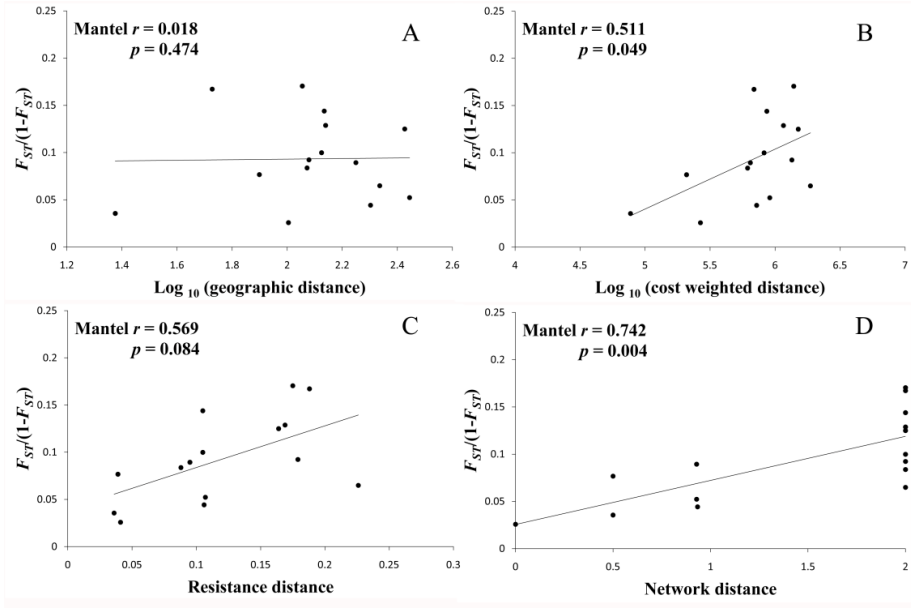

Fig. 4-4. Mantel correlations between matrices of linearized F_{ST} and matrices of log-transformed Euclidean distances (IBD; A), log-transformed least-cost distances (LCP; B), resistance distances (IBR; C), and network distances based on the threshold distance of 5 km (D).

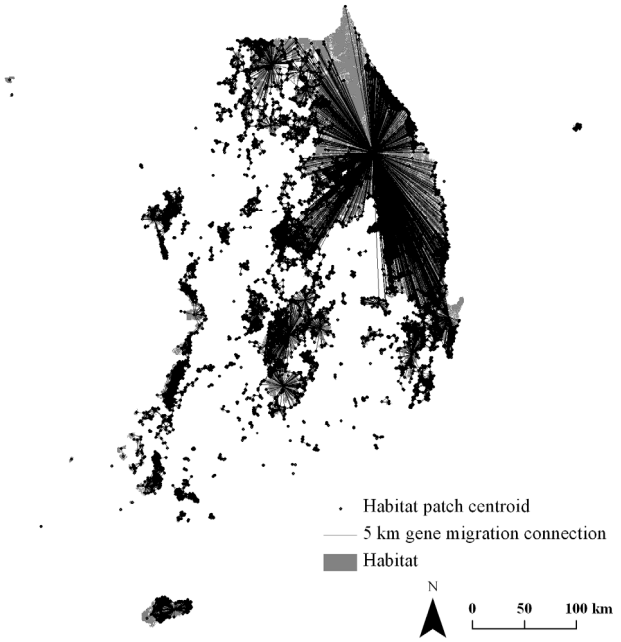

Fig. 4-5. Gene flow network of habitats for *K. septemlobus*. Habitat patches connected by black lines are assumed to be connected via gene migration based on a 5-km maximum distance.

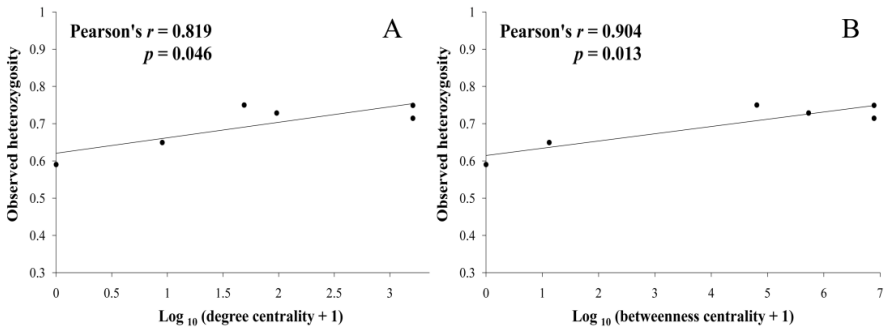

Fig. 4-6. Correlations between observed heterozygosity and centrality measures (A, degree; B, betweenness).

4.4 Discussion and conclusions

Assessing and maintaining connectivity and gene flow among fragmented populations are key components for ensuring the long-term persistence of species (Crooks and Sanjayan 2006). This study related habitat connectivity to the genetic structure of sparsely distributed tree *Kalopanax septemlobus* populations, characterized by a strong and significant genetic differentiation (Sakaguchi et al. 2012). In the study, the habitat of *K. septemlobus* was mainly determined by the gradient of annual mean temperature. Using habitat network analysis and partial Mantel tests to control IBD, LCP, and IBR predictions, the present work showed that *K. septemlobus* populations in a fragmented landscape had a spatial genetic structure, which is best explained by a network representation of habitat connectivity. This indicates that connectivity of habitat patches (i.e., structural connectivity) is an important element determining gene flow pathways (i.e., functional connectivity) for *K. septemlobus* in fragmented landscapes. In addition, their genetic structure and diversity was highly correlated with habitat connectivity at a scale of a few kilometers. These results emphasize the importance of landscape-level connectivity conservation in *K. septemlobus* metapopulations.

The Maxent model showed that annual mean temperature and slope were the two most important variables predicting habitat suitability for *K. septemlobus*, but variation in the annual mean temperatures explained more than 65% of the total variation in its ecological distribution. This concurs with a previous study suggesting that the ecological niche of this species is mainly constrained by a temperature component among the bioclimatic variables (e.g., Sakaguchi et al. 2010). In regard to slope, some studies also reported that *Kalopanax* stands were located in relatively steep-and ridge-slope areas (e.g., Kang and Lee 1998; Lee et al.

2000). Although the growth rate of *K. septemlobus* is high in low-slope valley areas where soil moisture and nutrient are rich, it is known that the species is usually overcome by other competitive tree species and released to ridge-slope areas (Lee and Kang 2002).

The predicted species distribution supported an earlier finding that *K. septemlobus* is widespread in temperate deciduous or coniferous forests of eastern South Korea (Fig. 4-2) (Lee and Kang 2002; Sakaguchi et al. 2012). However, based on the model's predictions *K. septemlobus* had a low probability of occurring (<0.2) in landscape areas with a moderate to a high mean annual temperature (10–17°C) (data not shown), indicating the species may become increasingly vulnerable to thermal stress associated with climate change (Allen et al. 2010). Moreover, suitable ranges of the species will shift northward as temperature increases (Sakaguchi et al. 2010). Thus, for such species a rise of the mean temperature in an unprecedented speed and scale due to human-induced climate change will become a severe stress, particularly when it suffers not only from a lack of capacity to move to another suitable habitat areas but also from a lack of gene flow among fragmented populations accompanied by the lessened capacity to adapt (Angert et al. 2011; Schloss et al. 2012). Further research is required to determine whether a range shift of *K. septemlobus* will keep pace with the shift in suitable ranges under climate change scenarios while considering the species dispersal ability.

Observed genetic differentiation among populations was quantified with different measures of distance: patch-based network distance vs. point-to-point isolation distances. A Mantel correlogram (Legendre and Fortin 1989) was used to explore the scale of autocorrelation between network and genetic distance. A significant positive correlation was found between genetic and network distances measured for threshold distances ranging from 1 km to 30 km (Fig. 4-3), indicating that gene flow is highly constrained by the scale-dependent habitat mosaic

structure. More importantly, regarding the values of Mantel coefficients, network distances calculated for a threshold distance between 4 and 5 km best explained the genetic structure of populations. This indicates the range of scales at which their genetic structure was most strongly associated with habitat connectivity, suggesting that the potential pollen- or seed-mediated gene flow is mainly restricted at a landscape scale, and rarely occurs at a regional scale (i.e., over distances of kilometers to tens of kilometers). Honey bees (*Apis* spp.) and bumble bees (*Bombus* spp.), the most frequent pollinators of *K. septemlobus*, have a foraging range of 1-5 km, sometimes very rarely up to 10-20 km when local resources are very scarce (Visscher and Seeley 1982; Sasaki 1999; Osborne et al. 2008; Pahl et al. 2011). Its seeds are dispersed by forest birds and the dispersal distance is estimated to be less than 100 m, according to a seed trap experiment (Iida and Nakashizuka 1998). Thus, the foraging behavior of wild bees may contribute to the gene flow among sparsely distributed *K. septemlobus* populations in the study area. In the meantime, bird dispersal of *K. septemlobus* seeds is known to be important in reaching a suitable habitat and escaping high mortality around conspecific trees (Iida and Nakashizuka 1998).

LCP and IBR predictions outperformed IBD by incorporating resistance values derived from habitat distribution modeling rather than straight-line distances (i.e., distances within undifferentiated landscape). These results indicate that habitat distribution and quality have important effects on the gene flow and the genetic structure of populations. Previous research shows that habitat preferences of species combined with landscape features influence dispersal patterns that modulate spatial population genetic structure (e.g., Castric et al. 2001; Row et al. 2010). However, the present study showed that network model had the highest simple significant correlation with genetic distance and outperformed all competing models, which is compelling evidence that the network is a more

accurate representation of gene flow across the landscape, and that habitat connectivity is an important factor in determining genetic structure in heterogeneous landscapes. In populations separated by long distances, the exact amount of movement between populations may not be as significant if there is at least one or few immigrants per generation that move into another population (Chang et al. 2001; Wang 2004). In addition, some studies showed that large continuous populations in regional landscapes with continuous and well-connected patches have either weak or no spatial genetic structure, indicating almost no genetic differentiation among them, regardless of the past demographic history (e.g., De-Lucas et al. 2009; Mayol et al. 2012). Thus, the component-based binary network model may be an appropriate metric to study long-term mixing of populations that focus on genetic transmission (Bodin and Saura 2010).

Fragmentation and habitat loss can reduce genetic diversity by limiting pollination and seed dispersal of plants and, thus, disrupting gene flow (Aguilar et al. 2008). In line with this explanation, population genetic diversity in the study was also positively correlated with both local and global topological strucures of a habitat mosaic at the 5 km scale (Fig. 4-6), implying that genetic diversity of populations is affected by connectivity of a habitat network and is likely to decrease with an increase of habitat fragmentation. In fact, previous meta-analysis concluded that genetic diversity is positively associated with population fitness (Reed and Frankham 2003) and that negative effects of habitat fragmentation on genetic diversity and fitness of plant populations are common (Leimu et al. 2006). As genetic diversity may reflect the species' adaptive potential in changing environments (McLachlan et al. 2007), reduced genetic diversity can inhibit population's ability to adapt and evolve in response to ecological perturbations associated with urbanization, climate change, exotic species, and disease spread (Spielman et al. 2004; Frankham et al. 2010). Thus, upholding habitat connectivity

is essential in maintaining high levels of genetic diversity that is necessary for population persistence in rapidly changing environments. Some studies show that with moderate or even relatively low levels of gene flow through pollen or seeds between fragmented populations, loss of genetic diversity can significantly be alleviated by preventing the effect of genetic drift (e.g., Sork et al. 1999; Couvet 2002).

Populations may tend to change their genetic structures rather slowly over time (Emigh and Pollak 1979) and past habitat connectivity may partially influence the genetic structure of the current populations (Münzbergová et al. 2012). This implies that the effects of the present-day landscape structure should be interpreted with caution while considering time lags of other possible effects on a genetic response of populations to landscape structure.

The method used to assess habitat connectivity is derived from a patch-based landscape graph approach where landscape connectivity is modeled by constructing a graph (also called a network) describing the dispersal or the degree of movement between a pair of habitat patches (Urban and Keitt 2001; Galpern et al. 2011). Graphs could provide a simple and effective means of representing the overall spatial structure of a habitat mosaic in terms of metapopulation structure of species in a fragmented landscape (Urban et al. 2009). To explore the interaction of organism–landscape in relation to movement and gene flow, a priori assumptions about a species' movement patterns and dispersal capacity are required, based on empirical studies that compare dispersal or daily movement tendencies in landscapes with different degrees of fragmentation. A graph theoretic approach, in this regard, enables a test of a model at multiple scales in order to identify critical spatial scales associated with the effect of landscape structure on metapopulation structures and movement patterns through performing edge thresholding (Bunn et al. 2000). While species responses to landscape structure vary depending on the

spatial scale, the dispersal capacity of species is often unknown. Thus, when considering functional connectivity, which explains a function of both responses of organisms and landscape structure, multi-scale landscape graph analysis is a robust approach to examine how functional connectivity changes at multi-scales.

The modeling approach applied here can be criticized for considering simple Euclidean (straight-line) distances connecting habitat patches. Dispersal and gene flow are rarely restricted to a single straight-line or an optimal pathway, and models that included multiple pathways have been shown to outperform single-path models in predicting population genetic structure (e.g., McRae 2006; McRae et al. 2008). Component-based habitat network analysis using Euclidean distance can perform better, but the predictive power of the method can be improved by incorporating not only matrix effects that represent barriers to gene flow but also multiple movement pathways that greatly improves habitat connectivity (McRae et al. 2008; Galpern et al. 2012).

This study employed network analysis combined with habitat distribution modeling to assess habitat connectivity and to evaluate how such connectivity may affect genetic structure and diversity of *K. septemlobus* populations. It appears that habitat connectivity has a strong positive impact on the gene flow of *K. septemlobus* populations and also on their genetic diversity. Hence, these finding not only highlight the importance of habitat connectivity, but also indicate that reduced connectivity due to continued landscape-scale habitat fragmentation and climate change may decrease the population genetic diversity, which, in turn, may alter the evolutionary potential for adaptation to their changing environments (Mayol et al. 2012). These results suggest that the conservation management strategy aiming to maximize the genetic diversity of *K. septemlobus* populations and the genetic diversity of other sparsely distributed plant populations should seek to maintain connectivity of habitat networks. This study may contribute to

developing methodological frameworks so that the interaction between habitat connectivity and ecological processes can be further investigated to better guide conservation and restoration plans.

5. Conclusions

The main focus of this dissertation was to elucidate the role of habitat connectivity in ecological processes, including movement, dispersal, and gene flow, which are involved in shaping biodiversity, by using multi-scale network approaches. This chapter presents a summary of the key findings from three linked studies and their implications for biodiversity conservation. Finally, recommendations for the future direction of research, given these findings presented herein, are provided.

5.1 Summary and implications

In this dissertation, habitat connectivity for various species was examined at multiple spatial scales. The major conclusions with regard to the primary goal of this dissertation were as follows: (1) habitat connectivity had a positive impact on biodiversity at two levels (i.e., the number of species and genetic variation) across different taxonomic groups (e.g., forest bird and tree species in Chapters 2 and 4, respectively) and (2) the most important factor for predicting roadkill of forest mammal species, which signals a threat to biodiversity, was the degree of intersected, thus disrupted, connectivity of protected forest area networks owing to roadways (see Chapter 3). Therefore, maintaining habitat connectivity across a variety of scales is important for the maintenance of biodiversity in birds, mammals, and populations of a threatened tree species (e.g., *Kalopanax septemlobus*).

My research has also shown that graph-based, multi-scale network models are effective at examining the functional relationships between habitat connectivity, ecological processes, and biodiversity. The network–theoretic approaches applied to investigate these relationships in this dissertation were cost-effective and,

especially in combination with available empirical data on species distribution patterns from national pilot studies, offered ecologically relevant indications of species responses to landscape structure and habitat fragmentation.

In Chapter 2, I examined how local habitat characteristics, human disturbance, and landscape connectivity influence the diversity of forest bird communities of small forest patches embedded in an urbanized landscape. The results suggest that bird diversity in urban areas could be enriched by small patches (i.e., less than 20 ha). Large green spaces can often support more species than do small ones. However, in practice, both budgetary and spatial constraints often prevent large-scale conservation efforts (Loss et al. 2009). Therefore, in such situations, preserving and creating small patches may provide opportunities for enhancing urban biodiversity (Loss et al. 2009; Shwartz et al. 2013). In addition to providing nesting habitats for breeding birds, small patches are important as stop-over sites (i.e., stepping stones) that contribute to regional habitat connectivity for migrant bird species (Brawn and Stotz 2001).

The diversity of urban forest birds was influenced strongly by patch area, human disturbance, and, to a lesser extent, habitat complexity (i.e., habitat diversity) and connectivity. In other words, local-scale structural variables and human disturbance had more influence on bird species diversity in urban forest fragments than landscape-scale effects. Thus, when planning urban biodiversity conservation and habitat management in urban areas, it is necessary to first address improvements in the local habitat structure through increased patch size and reduced human access, which can contribute to local-level species diversity. Secondly, at the patch scale, management to increase habitat complexity is also necessary for preserving high, local diversity of forest birds. Structurally complex habitats, including diverse tree species and large-diameter trees (with multiple canopy layers and abundant coarse woody debris), may provide more niche spaces

and alternative ways of exploiting natural resources, and thus, may support high avian biodiversity. Third, connectivity among habitats should be maintained in order to increase species diversity and the resilience of urban habitat networks. Therefore, for developing highly resilient habitat networks, management strategies require the identification of crucial regions for connectivity and gaps to restore connectivity between existing urban forest fragments.

In Chapter 3, I investigated the influence of the connectivity of protected forest area networks, road features, and landscape characteristics on roadkill abundance of small, intermediate, and large mammal groups. The effect of highways and rivers, which can act as barriers to the movements of mammals, on the protected forest area network was also analyzed. In all three mammal groups, the number of roadkill increased as more roadways intersected with connectivity pathways, thus, showing that roadkills primarily occur on roads that intersect high-connectivity routes. These data also highlight the importance of maintaining connectivity at multiple scales. These findings show that adherence to a single-species or -group management strategy for developing a framework that will restore the ecological connectivity network is unlikely to benefit the overall biodiversity.

Habitat networks were well connected for large mammals, but not for mammals of intermediate and small sizes. However, habitat connectivity of forest mammals, especially with large home ranges and distant movements, were greatly reduced when highways were included in the network analysis. Overall, these results indicate that different conservation strategies for connectivity should be implemented to decrease the number of roadkill for different groups of species and, in turn, to increase the likelihood of their persistence. For the conservation of small mammals, creating additional habitats should be considered so that they could offer recourses and shelter for the colonization and connect existing core habitats. Large

mammal conservation would benefit from the creation or restoration of corridor linkages among their core habitats by identifying areas where road segments intersect high levels of habitat connectivity, and then, building new wildlife crossings and fences. Then, animals could be funneled into these crossings, and wildlife warning signs to alert motorists in high-priority areas could be installed.

In Chapter 4, I investigated the relationships between habitat connectivity and gene flow for populations of a threatened tree, *K. septemlobus*. Annual mean temperature was the most important determinant of species distribution, indicating that species may become vulnerable to thermal stress under future climate change. Using graph-based habitat network analyses and partial Mantel tests to control predictions of conventional gene flow-models (e.g., IBD, LCP, and IBR), I showed that the spatial genetic structure within sparsely distributed populations of *K. septemlobus* is best explained by a network representation of habitat connectivity. This indicates that the degree of habitat patch connectivity (i.e., structural connectivity) is an important element that determines pathways of pollen-mediated gene flow (i.e., functional connectivity) for *K. septemlobus* in fragmented landscapes.

Population structure and genetic diversity were highly and positively related to landscape-scale (i.e., a few kilometers) habitat connectivity. This indicates that the spatial configuration of habitats at the landscape scale is important in determining population structure. The current habitat network was well connected for landscape-scale gene flow, but climate change is expected to severely reduce future levels of habitat connectivity and gene flow. Thus, it is crucial to regulate the over-exploitation of species and consider habitat connectivity improvement for sustaining populations. Overall, this study has important implications for identifying habitat bottlenecks and increasing functional, genetic connectivity when faced with critical threats from both habitat

fragmentation and rapid climate change. In addition, it emphasizes the importance of landscape-scale connectivity conservation in *K. septemlobus* metapopulations.

5.2 Future research directions

Preserving and restoring existing habitats and providing linkages among these habitats are critically important for species survival (Rudnick et al. 2012). However, it is still unknown how landscape connectivity affects broad-scale ecological processes underlying the dynamics of the coexistence of species, (i.e., a metacommunity). A metacommunity is defined as a set of local communities contained within patches that are connected by the dispersal of multiple potentially interacting species (Leibold and Miller 2004). In order to ensure the long-term persistence of biodiversity, conservation planning designed to increase the resilience of reserve networks needs to promote connectivity for metacommunities consisting of a broad suite of species with divergent life histories and habitat requirements. This means that well-connected landscapes for umbrella species should also provide extensive habitat connectivity for many other species and taxa (Roberge and Angelstam 2004). Hence, beyond the metapopulation concept, understanding the mechanisms that enable the coexistence of species across interaction types, including predation, competition, and mutualism between species; and how the varying levels of connectivity are related to metacommunity dynamics are the central challenges in biodiversity conservation. Some studies recently show, theoretically, that increased connectivity does not similarly benefit both predator and prey species, suggesting that an intermediate level of connectivity may be more desirable for conservation purposes (e.g., Baggio et al. 2011). More empirically oriented studies would be needed to understand the interactions in multi-species communities within habitat networks and their response to natural

and anthropogenic disturbances, and thus, to identify an optimum level of connectivity for both the persistence of the metapopulation and metacommunity.

Understanding habitat network dynamics is important for relating network patterns to ecological processes that regulate the abundance and coexistence of species. Despite changes in ecosystems over time, resulting mainly from human activities, and the fact that altered ecological processes function across multiple time scales (Dale et al. 2000), the bulk of connectivity studies are static descriptions of habitat network structures. In addition, to date, few studies have analyzed the temporal dynamics of connectivity networks (e.g., Olesen et al. 2008). Quantifying connectivity at a snapshot in time and relating it to empirical observations of species distributions assume a static landscape structure, ignoring the temporal heterogeneity of disturbance. Although static network modeling is a necessary first step, given the data with insufficient time-lag and limited models available, the static models may have limited predictive power (Wiens 1997; Wimberly 2006). Studying the temporal dynamics of habitat networks and developing spatio-temporal network models, therefore, are key areas of future research needed to improve the management of fragmented dynamic landscapes for the maintenance of long-term connectivity.

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국문초록

파편화된 경관에서 서식지 연결성을 평가하고 유지하는 것은 생물종 보전을 위한 핵심적인 요소이다. 그러나 국내에서 생물종 다양성과 관련되어 있는 연결성 정도가 얼마인지, 서식지 연결성이 생물종 전파와 유전자 흐름과 같은 생태과정을 유지시킬 수 있는 연결성을 가지고 있는지에 대해서 충분히 검토하지 못했다.

이 연구에서는 서식지 연결성이 생물 군집의 다양성과 이동뿐만 아니라, 개체군의 유전적 다양성과 어떤 관계가 있는지 분석하기 위해 산림성 조류와 포유동물 군집, 음나무 개체군을 연구 대상으로 하였다. 산림성 조류는 이동성에 제한을 덜 받지만, 포유동물의 이동성은 도로 등에 큰 제한을 받고, 반면 음나무 개체군의 이동은 종자전파 조류종 또는 수분매개 곤충에 의해 가능하다. 이들 생물종은 육상생태계의 생물다양성을 대표하며, 생태계 서비스에서 중요한 역할을 하고 보전 가치가 높지만, 도시화 등 인간의 활동으로 인해 생존에 큰 위협을 받고 있다.

생물종별 요구되는 최소 서식지 면적과 이동능력이 다르기 때문에 경관 구조에 대한 반응도 다양하게 나타난다. 따라서 생물종별 서식지 특성을 고려하면서 다양한 공간규모에서의 서식지 연결성이 종 분포와 이동, 생물다양성에 끼치는 영향을 분석하기 위해 그래프 이론에 기반한 네트워크 분석 방법론들이 다변량 통계기법과 함께 적용되었다. 첫째, 서울시와 인근 주변도시(고양시, 부천시, 광명시, 구리시 등)에서 산림성 조류종 분포와 서식지 환경조사를 통해 서식지 구조와 연결성, 인간간섭이 조류 다양성과 길드별 서식지 선택에 끼치는 영향을 분석하였다. 둘째, 산림보전지역을 대상으로 도로가 차단하는 연결성 정도와 도로와 주변 지형경관의 특징 등이 소·중·대형 포유동물 군집들의 로드킬 발생률과 어떤 관계가 있는지 밝히고, 도로와 강 같은 인위적·자연적 장애물이 전체 서식지 연결망에 끼치는 영향을 분석하였다. 셋째, 기후와 지형 등 다양한 공간환경변수를 이용하여

음나무 서식지를 도출하고, 서식지 연결성이 개체군 간 유전자 흐름, 유전적 다양성과 어떤 관계를 가지고 있는지 다중공간 규모에서 분석하였다.

서식지 면적이 클수록 전체 조류종수와 개체수, 수관과 나무구멍, 관목에 둥지를 짓는 종, 서식지 내부종과 가장자리종 등의 개체수가 높았고, 서식지 면적은 전체 조류종수와 개체수를 결정하는 데 있어 가장 중요한 변수로 나타났다. 서식지 다양성은 전체 조류종수와 철새 개체수, 지면에 둥지를 짓는 개체수에 영향을 끼쳤다. 인위적으로 조성된 숲에 비해 자연형 잔존산림숲에서 전체 조류종수와 개체수, 텃새 개체수, 곤충을 먹이로 먹는 종과 가장자리종 등의 개체수가 더 많았다. 500 m 규모에서 측정된 서식지 연결성이 높을수록 전체 조류개체수와 함께 텃새, 덤불에 둥지를 만드는 종, 곤충을 먹이로 먹는 종, 가장자리종의 개체수가 증가했다. 도시 산림성 조류의 다양성 보전을 위해서는 작은 녹지 면적을 늘리고, 인간간섭의 영향을 줄이는 것이 필요하다. 또한 서식지 다양성을 높이면서, 도시 내 파편화된 산림의 연결성을 유지하고 향상시키는 전략이 필요하다.

산림보전지역의 연결성을 많이 차단하는 도로일수록 소·중·대형 포유동물들의 로드킬 발생 수가 증가하는 것으로 나타났다. 연결성이 높은 지역에서는 포유동물들의 이동이 많은데, 이러한 지역에 도로가 위치하여 포유동물들이 도로를 건너다 차량에 의해 많은 로드킬을 당하는 것으로 판단된다. 도로와 큰 강과 같은 장애물 효과를 고려하지 않았을 때는 산림보전지역의 연결망이 대형동물에게는 잘 연결된 것으로 나타났지만, 소·중형 포유동물에게는 그렇지 않았다. 그러나 장애물 효과를 고려했을 때는, 특히 이동능력이 큰 대형 포유동물의 연결성이 가장 많이 감소되는 것으로 나타났다. 따라서 소형 포유동물에게는 파편화된 핵심 서식지들을 연결시킬 수 있는 새로운 서식지를 조성해주는 전략이 필요하다. 대형동물에게는 연결성을 많이 차단하는 도로구간과 강에 우선적으로 생태통로를 설치하여 안정적인 이동성을 확보해 주어야 한다.

음나무 서식지 분포에 가장 영향을 끼치는 환경인자는 연평균 기온으로 나타났다. 음나무 개체군의 유전적 구조와 차이는 경관규모 4~5 km에서의 서식지 연결망 거리에 의해 가장 잘 설명되었고, 또한 이 규모에서의 연결성은 개체군 유전자 다양성과 유의한 양의 상관관계를 나타냈다. 연구에서 제시된 방법론을 적용하여 서식지 파편화와 기후·환경변화에 취약한 생물종의 서식지 연결성과 유전자 흐름의 관계를 밝히고, 중요 공간규모에서 서식지 연결망을 유지하고 향상해야 한다. 이는 메타개체군 간 유전자 흐름을 원활히 하고 유전적 다양성을 확보하여, 미래 기후·환경변화에 대한 적응성을 향상시키는 데 매우 중요할 것이다.

세 가지 네트워크 분석 연구들을 통해 생물다양성 보전과 환경계획 수립에 있어 중요한 경관생태적 함의를 도출할 수 있다. 산림성 조류군집과 포유동물, 음나무 개체군은 이동능력과 전파특징이 각각 다르지만, 종 또는 군집의 서식지 선호도와 이동능력에 따른 공간규모를 고려하여 도출된 서식지 연결성은 이들 생물들의 분포와 이동, 유전자 흐름을 결정하는 중요한 인자임을 의미한다. 이는 경관이 생물종의 서식지 간 이동과 전파, 또는 유전자 흐름을 원활하게 하거나 방해하는 정도를 정량화는 것이 생물다양성 보전에 있어 중요한 의미를 지닌다는 것을 나타낸다. 또한 그래프 이론에 기반한 네트워크 분석 방법론들이 경관 연결성과 메타 개체군과 같은 생태적 과정 연구에 있어 효율적으로 적용될 수 있음을 보여준다. 서식지 파편화와 기후변화에 대비하여 장기적인 생물다양성 보전을 위해 다중공간 규모에서 서식지 연결성을 복원하고 유지하는 전략이 필요할 것이다.

주요어: 경관 연결성, 그래프 이론, 로드킬, 서식지 파편화, 유전자 흐름

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